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GEORGE H. F. NUTTALL, M.D., Ph.D., Sc.D., F.R.S.

Quick Professor of Biology in the University of Cambridge

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VOLUME XII SEPTEMBER, 1920 No. 3

MALFORMATIONS IN TICKS.

BY L. E. ROBINSON, A.R.C.Sc. (LOND.).

(*From the Quick Laboratory, University of Cambridge.*)

(With 5 Text-figures.)

IN 1909, and again in 1914, papers, recording cases of deformity in Ticks, were contributed to this journal, by Warburton and Nuttall[1], and Nuttall[2], respectively: since that time, numerous examples of malformation have been observed in the material examined by them and by myself, in the course of our collaboration in work on Ticks in general. Of these examples, the five which are described and figured below, are sufficiently striking to be placed on record. The figures have been drawn with the aid of the Abbe-Zeiss camera lucida, and, in each case, the degree of magnification is indicated by a scale representing a length of one millimetre.

Specimen 1.

Dermacentor atrosignatus Neumann, 1906, ♂, taken off a dog, at Kosempo, Formosa, collector's name not recorded. The specimen was received, on loan, from Prof. L. G. Neumann, and was derived, in the first instance, from the collection of the Deutsches Entomologisches Museum, Berlin. With the exception of the hypostome, the tick is normal in all respects. The hypostome shows a considerable degree of asymmetry, due to an antero-mesial displacement of the denticles on the left side. The non-denticular proximal portion exhibits an anomalous feature, in that it bears three forwardly-directed salient points; these are clearly displayed in the figure.

Specimen 2.

Amblyomma hebraeum Koch, 1844, ♀ (N. 2413 *a*). The specimen was found on a cow (28. VII. 1913), at Namahacha, Portuguese East Africa, and is the gift of Dr J. B. Botelho. The scutum is not only deformed, but is remarkably small for the species, its length measuring barely two-thirds of the length of a normal example. The eye is absent on the left side, and, immediately

[1] Warburton, C. and Nuttall, G. H. F. (1909), On new species of Ixodidae, etc., *Parasitology*, II. 57–76.

[2] Nuttall, G. H. F. (1915), Tick abnormalities, *Ibid.* VII. 250–257.

posterior to the site which it should occupy, the scutal margin is eroded by a striated cicatrix, which extends in a postero-lateral direction over the general

Fig. 1. *Dermacentor atrosignatus* ♂. Abnormal: deformity of the hypostome. (L.E.R.)

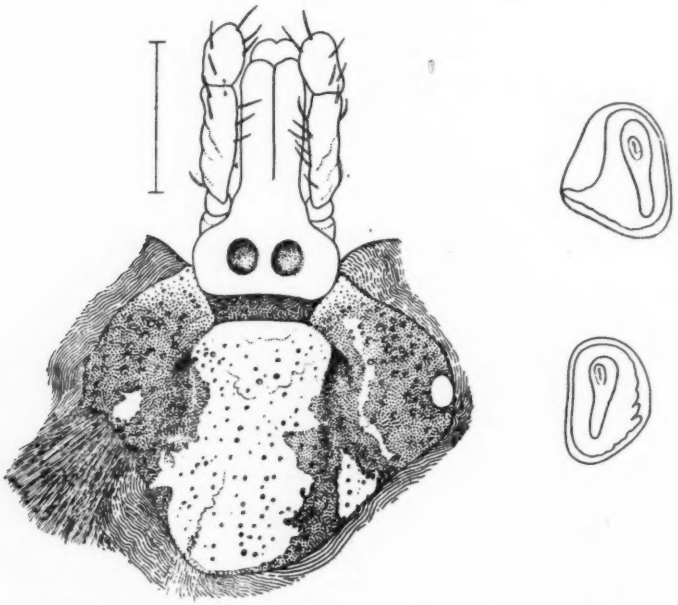

Fig. 2. *Amblyomma hebraeum* ♀. Abnormal: absence of left eye, and deformity of scutum and spiracle. (L.E.R.)

body integument. The left spiracle, although widely separated from this cicatrix by an extent of normal cuticle, is also deformed (see the lower of

the two figures of the spiracle; the uppermost figure represents the right spiracle of the specimen, which presents a normal appearance).

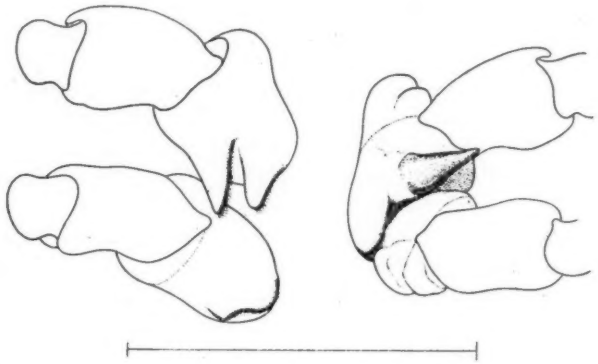

Fig. 3. *Amblyomma cajennense* ♂. Abnormal: fusion of coxae i and ii, with suppression of normal coxal armature. (L.E.R.)

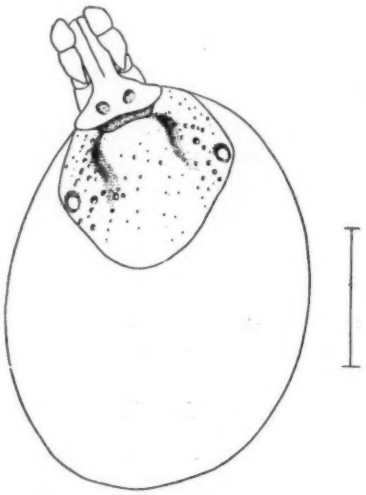

Fig. 4. *Hyalomma aegyptium* ♀. Abnormal: oblique curvature of body axis. (L.E.R.)

Specimen 3.

Amblyomma cajennense (F.), ♂ (ex N. 1654). This specimen was included with examples of *Ambl. coelebs* Nn., in a tube of ticks received from the Liverpool School of Tropical Medicine, labelled "No. 144," but with no other data. The specimen shows a fusion of the 1st and 2nd coxae on the left side:

the coxal armature of both is reduced to a single, stout, conical spur, which projects almost perpendicularly from the ventral surface. The corresponding coxae of the opposite side are normal, and are figured for the purpose of comparison.

Specimen 4.

Hyalomma aegyptium (L.), ♀ (N. 3347), off *Hemitragus hilocrius*, Cochin State, Madras, India; received from the Indian Museum, Calcutta. The specimen presents a considerable degree of asymmetry, due to an oblique curvature of the axis of the body. This is the most frequently occurring type of malformation in ticks. The fact that the scutum is also malformed, would appear to exclude the possibility that the distortion has been caused by unequal distension during the act of engorgement, a cause to which the condition often may be attributed.

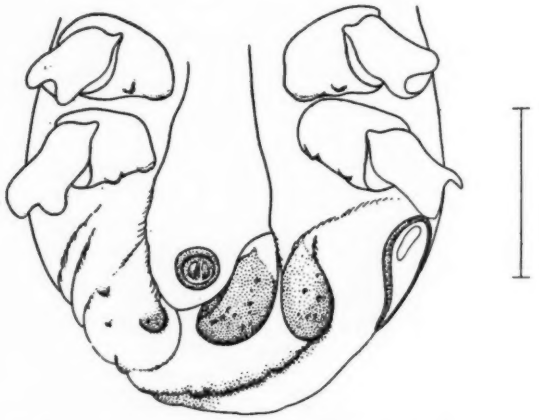

Fig. 5. *Hyalomma aegyptium* ♂. Abnormal: suppression of spiracle and adanal shields on right side of body. (L.E.R.)

Specimen 5.

Hyalomma aegyptium (L.), ♂ (N. 26 *c*), off goat, Germiston, Transvaal, S. Africa, 6. IV. 1918. The specimen was sent by Dr B. G. Brock. The posterior portion of the body is asymmetrical; the right spiracle is completely absent, and the adanal shields are reduced to vestiges on the right side. On the left side of the body, all of these structures are normal.

Such malformations as those described above, are probably the result of some mutilation of the tick during the course of the preceding nymphal phase. Experimental investigations of the power of regeneration of injured or amputated appendages, as manifested by ticks, have shown that this

power is developed to a high degree in the Ixodid ticks[1] especially, and to a smaller degree in the Argasid ticks[2]. In the course of engorgement, particularly as the state of repletion is approached, the chances of injury to which a tick is exposed are numerous, owing to the intentional or accidental scratching and rubbing of the infested parts of its body by the host, and the remarkable power of regeneration of damaged or lost appendages which the Ticks, in common with some other Arthropods, have developed, must ensure the survival of many individuals which otherwise would perish.

[1] Nuttall, G. H. F. (1920), Regeneration in Ticks. *Parasitology*, XII. 7–26.
[2] Hindle, E. and Cunliffe, N. (1914), Regeneration in *Argas persicus*. *Ibid.* VI. 353–371.

A MALARIA SURVEY IN THE MALAY ARCHIPELAGO.

By N. H. SWELLENGREBEL, Ph.D.

and J. M. H. SWELLENGREBEL-DE GRAAF, *Amsterdam.*

(*From the Institute of Tropical Hygiene, Amsterdam.*)

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INTRODUCTION.

The great discovery of Sir Ronald Ross has not led to the suppression of malaria in the Netherlands' East Indian Colonies, where the disease is still all too prevalent. The failure is partly, if not wholly, due to the mistake that has been made in considering the facts revealed by this discovery as an all sufficient basis for practical sanitary measures, whereas they can only serve as a foundation for further research in which special and local conditions are taken into account, with the object of acquiring information which is essential for the success of a sanitary campaign.

Local research has been much hampered by the confusion which has existed in the nomenclature of the various Anopheline species of the Malay Archipelago, a confusion due, no doubt, to entomologists, notably Dönitz and Theobald, having worked at the subject more or less independently. This lack of coordination gave rise to a confusion which rendered the subject almost unapproachable for the ordinary medical man. Apart from specimens preserved in European museums, nothing was known concerning our Anopheline fauna, and especially notable was our ignorance regarding the infectability of the various species with malarial parasites. Ignorance of these essential data made successful anti-malaria measures impossible because we undertook the impossible task of abolishing all Anopheline breeding places. The number, variety, and extensive distribution of these breeding places, including waggon tracks, hoof-prints, and other small depressions, of constant occurrence, even on well drained land, during the rainy season, made effective petrolisation impracticable. Could this difficulty have been surmounted, there still remained the most extensive breeding places of all, the rice fields. These furnish the

staple food for over thirty millions of inhabitants, and can neither be abolished nor petrolised.

The problem offered little prospect of solution, until we became acquainted with Watson's results (1911) in the Federated Malay States. His campaign was preceded by a thorough systematical and biological investigation of the local Anopheline fauna, and from the knowledge thus acquired, it was possible to conduct repressive operations against selected species.

Encouraged by Watson's success, Schüffner and Swellengrebel (1914) began to study the Anopheline fauna of the Malay Archipelago, with the result that our knowledge of the local species is now fairly complete[1].

The Anopheline genera and species of the Malay Archipelago are as follows:

GENUS.	SPECIES.
Myzomyia.	*ludlowi, rossii, indefinita, minima, minima* var. *aconita, flava*.*
Neomyzomyia.	*leucosphyra, punctulata (tesselata).*
Nyssorhynchus.	*fuliginosus, maculatus, jamesii*, schüffnerii*, annulipes* var. *moluccensis*.*
Cellia.	*kochii.*
Myzorhynchus.	*gigas, sinensis, sinensis* var. *vanus, sinensis* var. *separatus, barbirostris, barbirostris* var. *pallidus*, umbrosus, umbrosus* X (Watson), *albotaeniatus, mauritianus*.*
Stegomyia.	*aitkenii, aitkenii* var. *insulae florum*, aitkenii* var. *papuae*.*

The species marked with an asterisk are not recorded from the Malay Peninsula, while the following species have not hitherto been found in our Colonies:

Mennemyia brevipalpis, Lophoscelomyia asiatica, Pyretophorus watsonii, Myzomyia aurirostris, and *Myzorhynchus albotaeniatus* var. *montanus.*

Reverting to Watson's researches mentioned above, we find that in the hills of the Malay Peninsula, many difficulties have still to be overcome, but in the lowlands sanitary measures have become comparatively easy, as a result of these researches. Of the Anophelines found in the Malay Peninsula, only *Myzorhynchus umbrosus* is an important vector; its larva is peculiar, in that it only breeds in pools in the jungle. If these pools were abolished, malaria would be abolished, without incurring the expense and trouble which would be necessary in a general campaign directed against all species of Anophelines. This instance shows that eradication measures directed against selected species are profitable only under the following conditions:

(*a*) that one, or a very limited number of species are important vectors,

(*b*) that their breeding places are particular and restricted.

In the following pages we shall use the term "specific sanitation" to define anti-malarial measures directed against one or a few species, to the exclusion of those which are non-carriers or unimportant carriers. In drafting our programme of research in the Malay Archipelago, it was essential to discover:

[1] Schüffner and Swellengrebel (1914); Schüffner and Van der Heyden (1917); Swellengrebel (1914), (1916), (1917), (1918 *b*), (1919 *a*); Swellengrebel and Swellengrebel-de Graaf (1919 *b*); Winoto (1918).

(1) The species of Anophelines that are the principal vectors.

(2) The habitats of the larvae of these Anophelines.

Although it has been shown that the Anopheline fauna of the Peninsula and Archipelago are practically identical, we had doubts from the start, as to the advisability of applying without further investigation the results obtained in the Peninsula. This cautious attitude has proved to be justified.

In the following we shall constantly allude to the results of other investigators in the Malay Archipelago—Schüffner, v. Breemen, Bais, Citroen, and Winoto.

I. The Principal Vectors of Malaria in the Malay Archipelago.

At the commencement of our inquiry (February, 1917), data relating to this subject with respect to our Colonies, were scanty. Schüffner (1902) and de Vogel (1909) had succeeded in infecting mosquitoes, but unfortunately some doubt exists as to the species with which they experimented. We regard it as highly probable that Schüffner experimented with *M. ludlowi*, and de Vogel with *M. rossii*. As regards the Malay Peninsula, our information was more extensive, comprising, as it did, the results of the researches of Watson (1911), Stanton (1914), and Strickland (1916). We are also acquainted with the work of Walker and Barber (1914) in the Philippine Islands, and with that of Kinoshita (1906) in Formosa. Barber's paper (1918) made its appearance some months after the publication of our first paper. The authors I have cited indicate *M. umbrosus*, *N. maculatus*, *M. aconita*, *M. minima* (*febrifer*), and *M. sinensis* as the most dangerous species, but none of them appears to consider *M. ludlowi* as an important vector, although Christophers long ago proved it to be such in the Andaman Islands. Stanton is dubious on the subject, while Watson (1915, pp. 82–83) remarks "My feeling from what I have seen in the Federated Malay States is, that *A. ludlowi* can exist, without producing malaria, and indeed that malaria will disappear from a place where steps are taken which abolish only *A. umbrosus*—a proved carrier, yet leave very large numbers of *A. ludlowi*." Strickland considers it to be of importance, but only if it is very plentiful, contrary to the hill species which remain dangerous even when scanty. These opinions are interesting in the light of our own findings, which showed *M. ludlowi* to be the most important vector of all the Archipelagan species. This shows the indispensability of local researches. Had we neglected them by simply accepting the results obtained in neighbouring countries, we should have fallen into grave errors.

Whether or not a certain species is a good vector may be determined by (*a*) the direct and (*b*) the indirect method. For the present we shall consider the direct method only. This consists in determining the rate of infection with malaria parasites (*a*) in mosquitoes fed on gamete carriers (rate of experimental infectability or shortly "E. I.") or (*b*) in mosquitoes caught in nature (rate of natural infectability, in short "N. I."). Of the two methods, the first has found a much larger application, because it is more generally practicable.

It is often extremely difficult to procure mosquitoes in numbers sufficient for the determination of the N. I.; and, moreover, if they are found to be all uninfected, it may still be asked whether there was no flaw, and whether the species under examination is not after all a good vector. In experimental work no such doubt exists, provided the gamete carrier is a good one, and that another species, known to be a good vector, is used as a control. It is also easier to obtain large numbers of mosquitoes artificially bred than caught in nature. On the other hand, there are many factors which determine the chance of the mosquito becoming infected, and which are not taken into account in experimental work, and so do not influence the E. I., whereas they may materially affect the N. I. In this way it may happen that the determinations of E. I. and N. I. yield different results. Thus we found this to hold for *M. sinensis*, which was easily infected experimentally, but uniformly showed a low N. I. In this connection we may quote the observations recorded by Stephens and Christophers, and by James, which revealed a similar discordance between the N. I. and the E. I. of *M. rossii*. As to which of the two, the N. I. or the E. I., should be trusted in practice, the above-named observers unhesitatingly express a preference for the N. I. and we agree with them. Experiments show that under favourable conditions certain species may transmit malaria, but they leave us in doubt as to whether these conditions obtain in nature. Our observations may leave us uncertain whether under changed conditions a given species will or will not become a good vector, but at least they tell us that under the conditions existing in a given country, a particular species actually does or does not harbour malaria parasites. If such observations carried out in various localities, yield uniform results, the latter, in our opinion, are of more practical value than those obtained by experiment. *We have therefore adopted the determination of the N. I. as our standard method to discover the principal vectors* of malarial parasites, and, according to the conditions formulated above we have extended our researches to various localities.

The figures representing the N. I. of one and the same species in different places, all of them highly malarious during the period of observation, often show a marked divergence (Table III). One of the principal causes of this is the fact that gamete-carriers are more numerous and potent in regions of epidemic malaria, than in countries where endemic malaria prevails. Where there is endemic malaria, the spleen-rate is much the same in both children and adults, and it is invariably high (80 per cent. and more). The parasite-rate, in young children especially, is considerably higher than in adults. Comparing the rate of infection in children and adults, with the three species of malarial parasites separately, it appears that in adults, the three species do not disappear at the same rate, the decrease of simple tertian and quartan being more marked than subtertian. In the case of subtertian parasites, a striking feature may be noted, namely, that the decrease of crescents is greater than that of rings and the number of gametes present in the crescent-

carriers is often so small as to make it improbable that an Anopheline will become infected by the carriers' blood. In children, especially when young, both the rate of crescent-carriers and the number of gametes per carrier, are much higher.

In regions of epidemic malaria, during the course of an epidemic, the spleen-rates in children and adults are equal, and often reach a figure not less than that of the splenic index in endemic regions; but in this case, the parasite-rates in children and adults are likewise equal. No difference is to be noted in the rate of infection with the three species of malarial parasites, or in the percentage of crescent-carriers, or in the number of crescents or rings per carrier. The total number of infections is also much higher than in endemic regions.

Schüffner (1919 *a*) explains this difference by the immunity that is generally supposed to develop in a population continually exposed to malarial infection. In endemic regions this immunity is attained by the adults; in epidemic regions it is not attained because serious epidemics are generally too infrequent to allow of a lasting immunity being acquired.

The foregoing description of the relative parasitaemia in regions of endemic and epidemic malaria, is based on the most typical cases. It is obvious that, apart from these, numerous intermediate cases are to be met with, as may be gathered from the following table (Table I).

Table I.

Locality	Author and year of publication or delivery of report	Children or adults	Percentage of people examined showing infections of: Simple tertian	Quartan	Sub-tertian	Crescents	Spleen-rate
Tegal	Swellengrebel, 1919 *c*	child	8	3	32	15	91
(endemic)		adult	0	0	17	1·7	91
Mandailing	Schüffner, 1916–1917	child	6	11	25	9	96
(endemic)		adult	0·3	1	5·2	0·9	96
Semarang	Swellengrebel, 1918 *d*	child	8	4	15	10	80
(endemic)		adult	2·7	0·8	7	2·7	74
North Soendatar	Swellengrebel, 1918 *e*	child	21	9	68	48	90
(epidemic)		adult	11	4	53	34	87
Naras	Schüffner, 1919 *b*	child	35	3·5	65	40	84
(epidemic)		adult	24	2·3	55	36	70
South Soendatar	Swellengrebel, 1918 *c*	child	4	2	18	13	21
(epidemic)		adult	4	3	18	13	29

In regions of epidemic malaria, the number of carriers from which Anophelines can acquire infection is much greater, because of the many infected children *and* adults. In endemic regions the number of carriers is less, these being for the most part children alone. This should be taken into account when comparing the N. I. of the same species in different localities. Species usually exhibiting a very low N. I. may, in the epidemic regions, appear to be as heavily infected as good vectors in endemic regions. This is shown in the following table (Table II).

Table II.

Locality	*M. ludlowi*			*M. rossii*			Crescent rate	
	Examined	Infected	N. I.	Examined	Infected	N. I.	Adults	Children
Panggoeng	100	16	16	93	3	3	17	32
Pendjalan	185	10	5	243	1	0·4	1·7	15
Mandailing	4609	102	2·2	—	—	—	0·9	9

The rule of the N. I. being high in regions of endemic malaria, is not without exceptions. In Soendatar this figure was less than 1 per cent. in *N. fuliginosus* and *M. sinensis*, and zero in other species, such as *M. aconita* and *N. maculatus*. In Naras, Schüffner found 6 per cent. of *M. ludlowi* infected, whereas in other endemic regions we occasionally found as high a rate as 35 per cent. for the N. I. of this species. From this we infer the existence of still other factors, whose nature is as yet unknown, which influence the N. I.

When comparing the results of determinations of N. I. in different localities, much circumspection is necessary, unless a control, in the form of a known carrier, enables us to check our findings. The best species for control purposes is *M. ludlowi*, the only mosquito which is invariably found infected in all malarious districts.

In the following tables we have collected the results of several determinations of N. I. and E. I. together with records of blood and spleen examinations. In both sets of observations, it may be noted that at least one species of mosquito was found to be infected. We have excluded all observations in which this was not the case. For a comparison of the results obtained in the Malay Archipelago with those from neighbouring countries, we have added to these tables the figures of N. I. from Malacca and British North Borneo, and the figures of E. I. from Malacca.

Supposing the N. I. of a given species to have been determined in various districts, likewise the nature of the parasitaemia of the inhabitants, is it permissible from these data to draw any conclusions as to the economic importance of this species? As a rule we may do so provided the species is found infected in every locality, and that it shows a comparatively high degree of N. I. But, this condition is seldom fulfilled (excepting *M. ludlowi*). In the majority of cases the determination of N. I. still leaves some doubt as to the significance, from the sanitary standpoint, of the mosquito under observation. As an instance, in the district of Mandailing, we found that *M. ludlowi* showed the highest N. I.; but other species were likewise infected, *M. barbirostris* especially. What degree of importance is to be attached to this species? To find an answer we must look to neighbouring non-malarious regions, where *M. ludlowi* is absent, but where many of the species, which in Mandailing showed malarial infection, are present, notwithstanding a low N. I. Our experience in other localities has taught us that severe malaria never occurs with *M. barbirostris* as the only vector. From these three data we can infer

Table III. *Showing result of determination of N.I. in various localities of Java and Sumatra compared with similar figures from neighbouring countries.*

Locality	Observed by	*M. ludlowi*			*M. sinensis*			*M. barbirostris*			*M. indefinita*			*M. rossii*			*N. fuliginosus*			*N. punctulata*			*C. kochii*		
		Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection
Naras (Sumatra)	Schüffner, 1919 *b*	66	4	6·1	388	.	.	13	.	.	97	.	.	.	.	.	9	.	.	49	.	.	45	.	.
Angoli (Sumatra)	,, 1918 *b*	.	.	.	291	.	.	4	.	.	12	.	.	.	.	.	9	.	.	18	.	.	143	3	2·1
Western Java	Mangkoe Winoto, 1918	435	14	3·2	7	.	.	9	.	.	5	.	.	275	.	.	2	.	.	.	.	.	.	.	.
Batavia (Java)	v. Breemen, 1918–19	5120	82	1·6	.	.	.	9	.	.	34	.	.	2625	7	0·3	1	.	.	56	.	.	7	.	.
Siantar (Sumatra)	Bais, 1919	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sigiran (Sumatra)	Swellengrebel, 1918 *a*	6	1	16·6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Belawan (Sumatra)	Swellengrebel and Schüffner, 1919	679	34	5·0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Mandailing (Sumatra)	*id.*	4609	102	2·2	3606	4	0·1	544	3	0·5	2352	1	0·04	.	.	.	87	.	.	1380	.	.	474	.	.
Kepetakan (Java)	*id.*	177	63	35·0	273	1	0·4	23	.	.	12	.	.	141	1	0·7	1	.	.	1	.	.	.	.	.
Soerabaia (Java)	*id.*	740	69	9·3	.	.	.	.	.	.	53	.	.	573	3	0·5	.	.	.	.	.	.	.	.	.
Soendatar (Sumatra)	*id.*	.	.	.	701	1	0·1	6	.	.	115	.	.	.	.	.	569	2	0·3	10	.	.	66	.	.
Tegal (Java)	Swellengrebel, 1919 *c*	258	26	10·0	.	.	.	.	.	.	.	.	.	337	4	1·2	.	.	.	.	.	.	.	.	.
Semarang (Java)	,, 1918 *d*	1004	41	4·1	.	.	.	43	.	.	741	1	0·1	757	5	0·7	.	.	.	.	.	.	.	.	.
Modjowarno (Java)	,, 1919 *d*	.	.	.	3	.	.	31	.	.	300	1	0·3	3	.	.	13	.	.	139	1	0·7	62	.	.
Soerabaia (Java)	Reylingh, 1918	.	.	.	.	.	.	.	.	.	.	.	.	187	2	1·1	.	.	.	.	.	.	.	.	.
Mandailing (Sumatra)	Schüffner, 1916	30	2	6·7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Grand total		13124	438	3·3	5270	6	0·1	682	3	0·4	3721	3	0·08	4898	22	0·4	691	2	0·3	1553	1	0·06	799	3	0·4
Fed. Malay States	Stanton, 1914	.	.	.	87	2	2·4	16	.	.	114	.	.	.	.	.	23	1	4·3	.	.	.	7	.	.
id.	Barber, 1918	18	1	5·5	22	.	.	14	.	.	200*	.	.	.	.	.	4	.	.	3	.	.	6	.	.
id.	Watson, 1911	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
id.	Strickland, 1916	80	.	.	1	.	.	.	.	.	.	.	.	13	.	.	.	.	.	1	.	.	.	.	.
Brit. N. Borneo	Roper, 1914	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.
Grand total		98	1	1·0	110	2	1·8	30	.	.	314*	.	.	13	.	.	27	1	3·7	4	.	.	21	.	.

* Mixed *rossii* and *indefinita*.

Table III—*continued.*

Locality	Observed by	*M. aconita*			*N. maculatus*			*N. karwarii*			*N. leucosphyra*			*M. umbrosus*			*M. albotaeniatus*			*S. aitkenii*			Examination of children			Examination of adults		
		Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Dissected	Infected	Percentage of infection	Number examined	Spleen-rate	Crescent-rate	Number examined	Spleen-rate	Crescent-rate
Naras (Sumatra)	Schüffner, 1919 *b*	.	.	.	.	.	.	65	.	.	.	.	.	.	.	.	1	.	.	.	.	.	410	84	40	290	70	36
Angoli (Sumatra)	„ 1918 *b*	307	4	1·3	13	.	.	.	.	.	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Western Java	Mangkoe Winoto, 1918	96	7	7·3	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.
Batavia (Java)	v. Breemen, 1918–19	9	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Siantar (Sumatra)	Bais, 1919	.	.	.	.	.	.	.	.	.	235	4	1·7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sigiran (Sumatra)	Swellengrebel, 1918 *a*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Belawan (Sumatra)	Swellengrebel and Schüffner, 1919	.	.	.	.	.	.	.	.	.	.	.	.	28	1	3·6	.	.	.	.	.	.	114	87	13	.	.	.
Mandailing (Sumatra)	*id.*	1106	.	.	6	.	.	.	.	.	1	.	.	.	.	.	3	.	.	2	.	.	1056	96	9	709	96	0·9
Kepetakan (Java)	*id.*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	209	76	40	.	.	.
Soerabaia (Java)	*id.*	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	653	84–100	3–17	.	.	.
Soendatar (Sumatra)	*id.*	79	.	.	28	.	.	31	.	.	.	.	.	.	.	.	.	.	.	1	.	.	298	90	48	320	87	34
Tegal (Java)	Swellengrebel, 1919 *c*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	391	91	15	354	91	1·7
Semarang (Java)	„ 1918 *d*	41	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	262	80	10	601	74	2·7
Modjowarno (Java)	„ 1919 *d*	129	3	2·3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	197	37	10	184	32	13
Soerabaia (Java)	Reylingh, 1918	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mandailing (Sumatra)	Schüffner, 1916	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Grand total		1775	14	0·8	55	.	.	96	.	.	264	4	1·5	30	1	3·3	10	.	.	3	.	.						
Fed. Malay States	Stanton, 1914	78	3	3·8	32	2	6·2	20	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.
id.	Barber, 1918	66	.	.	11	1	9·1	60	.	.	.	.	.	261	6	2·3	.	.	.	.	.	.	.	.	.	.	.	.
id.	Watson, 1911	.	.	.	19	4	21·0	.	.	.	.	.	.	10	1	10·0	.	.	.	.	.	.	.	.	.	.	.	.
id.	Strickland, 1916	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brit. N. Borneo	Roper, 1914	.	.	.	.	.	.	.	.	.	17	.	.	130	1	0·8	.	.	.	.	.	.	.	.	.	.	.	.
Grand total		144	3	2·1	62	7	11·3	80	.	.	17	.	.	445	8	1·8	.	.	.	.	.	.						

N.B. The structure of the pigment of the Anophelines found infected in the Malay Archipelago was as follows:

	Fine pigment recorded	Coarse pigment recorded
ludlowi	176 times	188 times
rossii	11 „	7 „
leucosphyra	2 „	2 „
barbirostris	1 „	2 „
indefinita	2 „	1 „
sinensis	2 „	5 „
fuliginosus	1 „	1 „
aconita	1 „	2 „
punctulata	1 „	—

Table IV. *Showing summary of results of experiments at infecting the Anophelines of the Malay Archipelago with malarial parasites. For comparison the table also shows similar results obtained in the Malay peninsula.*

Experimentator	Variety of parasite. III. Simple tertian. IV. Quartan. P. Subtertian.	*M. ludlowi*		*M. sinensis*		*M. barbirostris*		*M. indefinita*		*M. rossii*		*N. fuliginosus*		*N. punctulata*		*C. kochii*		*M. aconita*		*N. maculatus*		*N. karwarii*		*N. leucosphyra*		*M. umbrosus*		*M. hunterii*		*M. albotaeniatus*	
		No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected	No. examined	Found infected
Swellengrebel, 1918 *a* / Swellengrebel and Schüffner, 1919	P.	37	37	292	15	10	.	7	.	.	.	.	.	23	1	5	.	.	.	.	.	.	.	3	.	87	.	.	.	6	.
Schüffner, 1918 *a*	,,	.	.	396	3	8	.	119	2	.	.	248	10	27	1	88	6	217	11	.	.	.	.	.	.	.	.	.	.	.	.
Total	,,	37	37	688	18	18	.	126	2	.	.	248	10	50	2	93	6	217	11	.	.	.	.	3	.	87	.	.	.	6	.
Percentage ...	,,	100 %		3 %		.		1·5 %		.		4 %		4 %		6 %		5 %		.		.		.		.		.		.	
Swellengrebel, 1918 *a* / Swellengrebel and Schüffner, 1919	III.	47	38	175	72	15	2	5	.	.	.	.	.	10	.	6	1	.	.	.	.	.	.	9	.	104	5	.	.	.	.
Bais, 1919	,,	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	9	.	.	.	.	.	.
Total	,,	47	38	175	72	15	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27	9	104	5	.	.	.	.
Percentage ...	,,	80 %		41 %		13 %		.		.		.		.		.		.		.		.		33 %		5 %		.		.	
Swellengrebel, 1918 *a* / Swellengrebel and Schüffner, 1919	IV.	107	5	182	2	1	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	6	.	.	.	1	.
Percentage ...	,,	5 %		1 %		.		.		.		.		.		.		.		.		.		.		.		.		.	
Grand total ...	,,	191	80	1051	92	34	2	139	2	.	.	248	10	70	2	105	8	217	11	.	.	.	.	32	9	197	5	.	.	13	.
Percentage ...	,,	42 %		9 %		6 %		1·4 %		.		4 %		3 %		8 %		5 %		.		.		28 %		2·5 %		.		.	
Stanton, 1914 (Fed. Malay States)	P.	.	.	11	.	8	.	22	.	.	.	10	2	.	.	4	.	22	9	7	1	.	.	.	.	5	.	.	.	.	.
Barber, 1918 (Fed. Malay States)	P. + III. but mainly P.	69	42	29	1	107	3	256	41	272	85	9	3	.	.	20	9	6	4	10	7	14	10	.	.	143	25	8	1	.	.
Grand total ...	,,	69	42	40	1	115	3	278	41	272	85	19	5	.	.	24	9	28	13	17	8	14	10	.	.	148	25	8	1	.	.
Percentage ...	,,	61 %		2·5 %		3 %		15 %		31 %		26 %		.		37 %		46 %		47 %		71 %		.		17 %		12·5 %		.	

that *M. barbirostris* is comparatively negligible as a cause of severe endemic or epidemic malaria.

This method of comparison, in neighbouring regions, of the parasitaemia and of the spleen-rate of the inhabitants, with the Anopheline fauna, enables us to ascertain the presence or absence of a correlation between the occurrence of a severe malaria and that of a particular species of Anopheline, and leads us to the determination of the *indirect index of infectivity* of this species, or shortly "indirect index" (I. I.). Taken alone, conclusions drawn from the I. I. are open to adverse criticism, but if the N. I. is likewise known, the conjoint data will furnish information as to the actual amount of damage done by the species.

Taking into consideration the figures given in Tables III and IV, together with the determinations of the I. I. for each species, we may summarize the facts as follows:

1. **M. ludlowi** is the most important vector of malaria in the Malay Archipelago, and shows the highest degree of N. I.; its importance is enhanced by the following propensities: the adult shows a preference for the interior of human dwellings; it usually occurs in large numbers; and it is able to cover by flight considerable distances. We have observed (1918 *c*) that large numbers of adults in nature habitually cover distances of 1·6 km., as measured in the direct line from the place of capture to the nearest breeding-place. We excluded all instances in which there was not absolute certainty of the absence of nearer breeding-places, and, moreover, all cases were excluded where only a few Anophelines could be found in the place of capture. Some small breeding-places might after all have been overlooked, and a few Anophelines might have been derived from this hypothetical breeding-place, but a number amounting to several hundreds could not be accounted for in this way. The majority were certainly derived from the extensive breeding-places under observation.

In two cases we succeeded in infecting Europeans with subtertian, by exposing them to the bites of *M. ludlowi*, which had been fed on a crescent-carrier twelve days previously. Ourselves being the subjects of this experiment, we are assured of the absence of any previous malaria infection. Moreover, the experiment was performed in a locality some 12 km. from the coast, where *M. ludlowi* was absent and malaria infection rare.

With few exceptions we found severe malaria to prevail wherever *M. ludlowi* was present.

2. **M. aconita** (including *M. minima*). Some doubt exists as to the ability of this species to transmit malaria. Winoto (1918) found it to possess the highest N. I. (7 per cent.) of all the species in very malarious hill-districts. We found it (1919 *b*) to be the cause of a rather severe epidemic in a previously non-malarious district, and exhibiting an N. I. of 2 per cent. In the highly malarious regions of Mandailing and Soendatar, however, we failed to

find infected females of *aconita*, only reputedly bad vectors, like *sinensis*, *barbirostris*, *indefinita*, and *fuliginosus*, were found infected. *M. aconita* was often found in districts where the incidence of malaria was insignificant. Attempts at experimental infection rarely succeeded (Schüffner). It seems therefore, that the infectivity of this species is subject to considerable variation, and its importance depends, to a large extent, on its occurrence in large numbers and throughout the year. If present in scanty numbers, or within the limits of particular seasons, it may cause epidemics of greater or less severity, but it does not seem to be capable of permanently raising the splenic index distinctly, as is the case with *M. ludlowi*, notwithstanding that the latter species shows a marked seasonal prevalence, and may be absent for a whole year. Although the importance of *M. aconita* should not be underrated, it is negligible in comparison with *M. ludlowi*.

3. **N. maculatus.** Infected specimens were never found, though sought for in highly malarious regions, where *M. sinensis* and *N. fuliginosus* showed infection (Soendatar), but the numbers examined were too small to allow of any definite conclusions being reached. On the other hand, the indirect index often points it out as a dangerous species, for its absence or presence in neighbouring districts, which otherwise possess a similar Anopheline fauna, coincides with the absence or presence of severe malaria. There are exceptions to this rule, however: in Siboga *N. maculatus* prevailed in the hills, while malaria was mainly confined to the seashore (*M. ludlowi*).

Here again, as with *M. aconita*, we must infer a high degree of variability in the power to rear malaria parasites on the part of the vector.

4. **N. leucosphyra.** Schüffner and Swellengrebel (1914) observed a distinct correlation between the appearance of this species and local outbreaks of malaria on tobacco estates and in certain coolie lines. Similar observations have been recorded by Roper (1914). Recently, Bais (1919) has confirmed and extended these observations by finding infected specimens (N. I. = 1·7 per cent.). He also succeeded in attempts at experimental infection with tertian parasites, the rate of infection, however, not surpassing that of *M. sinensis* as observed by us in some of our experiments (50 per cent.).

5. **M. sinensis** and **N. fuliginosus.** Both of these species were found infected in malarious regions, the former commonly so, but the N. I. was uniformly low (under 1 per cent.). Experimental infection of *M. sinensis* with tertian succeeded to a fairly high degree (at times over 50 per cent.); infections with subtertian and quartan were rarely successful. Experimental infection in man (with the same precautions as those taken with *M. ludlowi*) succeeded twice. *N. fuliginosus* was infected experimentally by Schüffner with subtertian (4 per cent.). The two species are common in both malarious and salubrious regions; in the former case obviously infected carriers are frequent. But in Soendatar, a region of severe malaria, we found them

to be the only Anophelines infected, all others, including *M. aconita* and *N. maculatus*, failing to show malaria parasites. In this case we must admit one or both of these species to be a possible vector, although the indirect index pointed to *N. maculatus* as being the principal vector.

6. **M. umbrosus.** This species was found infected but once. Experimental infection succeeded with tertian only, at a rate much below that of *M. sinensis*. Therefore *M. umbrosus* cannot be admitted as the cause of a severe epidemic, moreover, the indirect index never pointed to its being a dangerous species; still we mention it separately, because Watson (1911) considers it to be the chief vector in the plains of the Malay Peninsula, and Barber (1918) succeeded in infecting specimens from some localities and not from others. We presume therefore that its infectivity is variable, and it should, at least, be suspected. Nevertheless, *M. umbrosus* has not the importance which attaches to *M. aconita*, *N. maculatus* and *M. ludlowi*.

7. In this section we shall consider certain species with a relatively low N. I. (under 1 per cent.), although in epidemic regions the N. I. may rise to 3 per cent. (*M. rossii*). The species in question are *M. rossii*, *M. barbirostris*, *N. punctulata* (*tesselata*), and *M. indefinita*. These species are not confined to malarious regions. We are inclined to include *C. kochii* in this category although Schüffner (1918 *b*) once found it to be more highly infected than the presumed local vector (*M. aconita*).

All of these species have been infected experimentally, but it would appear as if natural infection of the vectors is small in regions of low endemicity owing to the paucity of gamete-carriers. Of the species enumerated, *M. indefinita* is the least important.

8. **S. aitkenii** (with its larval varieties *insulae florum* and *papuae*). Further information regarding this species is required. It was found exclusively in highly malarious regions associated either with *M. aconita*, *N. maculatus*, or *N. annulipes* var. *moluccensis*. The last species is the most common Anopheline in the eastern part of the Malay Archipelago; regarding its infectivity we can say nothing for the present. Furthermore we have failed to find natural infection in *M. flava*, *M. albotaeniatus*, *M. mauritianus*, *M. gigas*, *N. schüffnerii*, *N. jamesii*, and *N. kawarii*.

Arranging the above species with regard to their epidemiological significance, we obtain the following sequence:

(1) *Myzomyia ludlowi*; (2) *Myzomyia aconita*, *Nyssorhynchus maculatus*, (perhaps also *Stegomyia aitkenii*); (3) *Neomyzomyia leucosphyra*, *Myzorhynchus umbrosus*; (4) *Nyssorhynchus fuliginosus*, *Myzorhynchus sinensis* (? = No. 6); (5) *Cellia kochii*; (6) *Myzomyia rossii*, *Myzorhynchus barbirostris*, *Neomyzomyia punctulata* (*tesselata*); (7) *Myzomyia indefinita*.

II. Habitats of the Anopheline Larvae.

One of the conditions needed for the institution of specific sanitary measures, appears to hold in the Malay Archipelago. In all highly malarious districts studied hitherto, only one or two species are certainly or presumably principal vectors, and the remainder may be neglected. But are we justified in neglecting them? Is it possible to carry out sanitary works, directed against these known vectors, without including all other Anophelines in that locality? In other words, are the breeding-places of known vectors sufficiently differentiated to allow of "specific sanitation" (see p. 181)? This problem we must solve, otherwise our measures may prove useless.

A species may be particular in the choice of its breeding-place, or on the other hand it may show a considerable degree of adaptability in this respect. When observations are conducted in but one locality, it is often impossible to form a correct opinion on this subject, even after prolonged investigation. In the course of observations lasting nearly a year, we found (in Modjowarno, East Java) the larvae of *M. aconita* inhabiting rice-fields exclusively, and usually fields about to be harvested. In other localities this species was found to be more generally distributed (see Table V, p. 194).

The larvae of *N. maculatus* were found only in hilly districts; they are generally confined to little streams and springs on hill slopes. Consequently it might be supposed that sub-soil drainage, etc. would eliminate the larva. Unfortunately, we have noted abundant larvae of this species in a variety of waters (rice-fields, puddles, brackish pools near the seashore, cement tanks, etc.) during the dry season when the small streams above alluded to are dried up (see Table V).

The larvae of *M. umbrosus* occur in fresh and brackish water near the seashore and elsewhere, showing a preference for shade, but sometimes occurring in the open with no other protection against the sun than that afforded by short rushes. The larvae of *N. leucosphyra* on the other hand invariably affect shady pools, without discrimination in other particulars, the water being clean or muddy, stagnant or running. Our observations regarding the latter species are few (see Table V).

The larvae of most of the other species occur in a variety of waters. Some, like *M. aconita*, select one particular type, almost to exclusion of others; in Mandailing for instance, we found larvae of *M. barbirostris* frequenting fish-ponds, but comparatively rare in the rice-fields, where *M. sinensis* was the commonest larva. In other localities, however, *M. barbirostris* larvae were even more numerous in the rice-fields than were those of *M. sinensis*. This observation also applies to other species which are very particular in their choice of a breeding-place; in other districts they appear to be independent of special breeding grounds (see Table V).

A few species never leave us in doubt as to their dependence on particular breeding-places; some species are ubiquitous—*N. annulipes* var. *moluccensis*

may be found breeding in all imaginable collections of water (salt, brackish, fresh, dirty, clean, running or stagnant). In the absence of natural breeding sites, it will thrive in artificial ones (water in boats drawn up on shore, water in coconut shells, etc.) as readily as will *Culex fatigans* or *Stegomyia scutellaris*. The larva of *M. indefinita* behaves in a similar way, except that it is not often found in distinctly brackish water: we even found it breeding in saucers, of water, placed to prevent the access of ants. *C. kochii* and *N. punctulata* (*tesselata*), though somewhat more fastidious, distinctly belong to this group.

Still there are limits to the breeding possibilities of these species. In water, highly polluted with faecal matter, the larvae are absent; we once found *N. punctulata* in this situation (see Table V). Two species were found to be very limited in the choice of a breeding-place. The first of these, *S. aitkenii*, occurred in swiftly running mountain streams in 97 per cent. of cases. In this restriction of habitat it compares with what is stated concerning *N. maculatus*. If *S. aitkenii* proves to be a vector of malaria, this knowledge may be put to practical use. The second species, *M. ludlowi*, has at present a more practical importance. It is found in two morphologically indistinguishable varieties, which, on physiological grounds, must be dealt with separately. The first or *littoral form*, is almost confined to salt or brackish water along the coast, especially in places where algae (*Enteromorpha*, *Cladophora*, *Cyanophyceae*) and other filamentous aquatic plants, like *Najas*, are growing. In such breeding-places, during the dry season, June–September, the larva may be found in immense numbers. It is occasionally found in fresh water, but even then it is limited to the coastal zone, rarely penetrating inland for more than 4 km., except in such places where brackish water is to be found far inland (tidal rivers). Where the tide runs in and out freely, as in mangrove swamps, it appears to be absent; but if human intervention, by the construction of bunds, locks, etc., creates obstacles to the tidal water, the conditions change; grass begins to grow between the roots of the rhizophores, and larvae of *M. ludlowi* soon begin to appear. A place comparatively healthy before the commencement of the operation is thus rendered highly malarious (see Table V).

The larvae of the *inland form* of *M. ludlowi* are to be found only in the narrow valleys among the mountains running parallel to the west coast of Sumatra, where they occur in numerous fish-ponds. These ponds are almost the only breeding-places of this species, but it may breed in rice-fields also, though rarely. In one of the valleys, an extensive lake (Manindjau) is situated, along the banks of which this form is common among the rushes and algae, a frequent habitat of many Anopheline larvae (Table V).

Table V. *Showing the number and habitats of the several species of Anophelines together with the percentage frequency of each species in various breeding-places.*

Type of breeding-place	*M. ludlowi* littoral form		*M. rossii*		*M. ludlowi* inland form		*N. leucosphyra*		*M. umbrosus*		*M. indefinita*		*C. kochii*		*N. punctulata*		*M. sinensis*	
	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
I. NATURAL BREEDING-PLACES.																		
A. *In salt or brackish water.*																		
1. In fishponds	1282	54·5	2028	30·3	.	.	.	.	.	.	.	.	.	.	.	.	.	
2. Elsewhere	814	34·6	4339	64·9	.	.	.	.	141	51·1	103	2·2	6	1·9	26	3·3	58	0·6
B. *In fresh water.*																		
3. In immediate neighbourhood of sea coast ...	233	9·9	223	3·3	.	.	25	8·3	63	22·9	260	5·5	43	13·7	49	6·3	19	0·2
4. In rice-fields, in plains and hills	4	0·16	18	0·3	12	0·4	.	.	.	.	1291	27·4	34	10·9	272	35·0	4748	50·2
5. In little streams (running), their springs, marshes formed in their course, irrigation ditches for rice-fields	4	0·16	7	0·17	.	.	61	20·2	60	22·0	1006	21·3	43	13·7	102	13·1	1163	12·3
6. Marshes and pools, containing clear water, much overgrown	2	0·08	46	0·69	.	.	.	.	4	1·6	342	7·2	20	6·4	65	8·3	200	2·1
7. Fish-ponds (fresh water)	.	.	.	.	6022	97·9	.	.	.	.	808	17·1	66	21·4	47	6·0	2990	30·5
8. Pools in jungle...	.	.	.	.	.	.	216	71·5	2	0·8	.	.	26	8·3	135	17·3	.	.
9. Pools and small puddles with dirty water ...	.	.	.	.	.	.	.	.	.	.	899	19·1	75	23·7	82	10·7	283	3·0
10. Great inland lakes (along the shore) ...	.	.	.	.	108	1·7	.	.	.	.	3	0·08	.	.	.	.	.	.
II. ARTIFICIAL BREEDING-PLACES.																		
11. Cemented tanks, water in native boats, in coconut shells, earthenware saucers, etc.	14	0·6	23	0·34	.	.	.	.	4	1·6	4	0·12	.	.	.	.	1	0·01
Grand total...	2353	100	6684	100	6142	100	302	100	274	100	4716	100	313	100	778	100	9462	100

Table V—*continued.*

Type of breeding-place	*N. fuliginosus*		*M. barbirostris*		*S. aitkenii*		*M. aconita*		*N. maculatus*		*N. karwarii*		*M. albotaeniatus*		*N. annulipes* var. *moluccensis*	
	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
I. NATURAL BREEDING-PLACES.																
A. In salt or brackish water.																
1. In fishponds	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2. Elsewhere	5	0·3	60	0·6	1	0·7	.	.	.	.	.	.	.	.	174	29·4
B. In fresh water.																
3. In immediate neighbourhood of sea coast ...	31	1·9	90	1·0	.	.	.	.	1	0·2	.	.	.	.	135	22·8
4. In rice-fields, in plains and hills	262	16·1	929	10·2	3	1·9	782	45·0	46	8·0	.	.	.	.	.	.
5. In little streams (running), their springs, marshes formed in their course, irrigation ditches for rice-fields	375	23·1	1051	11·5	152	97·4	567	32·7	246	42·9	26	100	.	.	63	10·6
6. Marshes and pools, containing clear water, much overgrown	87	5·3	1326	14·5	.	.	119	6·8	189	33·0	.	.	.	.	115	19·4
7. Fish-ponds (fresh water)	844	51·9	5431	59·6	.	.	261	15·0	23	4·0	.	.	.	.	.	.
8. Pools in jungle...	.	.	36	0·4	.	.	.	.	.	.	.	.	37	100	15	2·5
9. Pools and small puddles with dirty water ...	18	1·1	175	1·9	.	.	7	0·5	34	6·0	.	.	.	.	36	6·1
10. Great inland lakes (along the shore) ...	2	0·2	3	0·07	.	.	.	.	.	.	.	.	.	.	.	.
II. ARTIFICIAL BREEDING-PLACES.																
11. Cemented tanks, water in native boats, in coconut shells, earthenware saucers, etc.	1	0·1	9	0·23	.	.	.	.	34	5·9	.	.	.	.	54	9·2
Grand total	1625	100	9110	100	156	100	1736	100	573	100	26	100	37	100	592	100

III. Practical importance of the larval habitat.

It is evident that this study possesses a more than academic importance. Let us imagine the effect which would be caused by an apparently unimportant change in the habitat of such a species as *M. ludlowi*, which we may suppose to acquire the breeding habits of *M. indefinita*. Such an occurrence in the Malay Archipelago would spell disaster. The severe endemic malaria, at present confined to the sea coast, and strictly localized in the interior, would lead to the spread of the disease over wide areas in a manner corresponding to what is seen in some parts of Africa. All this would result from an exchange of habitat between two Anophelines, so closely allied morphologically that some entomologists refuse to consider them as distinct species. Moreover, the eradication of the larvae would become a practical impossibility; for an Anopheline capable of breeding in all possible collections of water, in a country of high humidity and heavy rainfall, and where the population is dependent on the cultivation of rice, cannot be abolished.

Although conditions in the Malay Archipelago are not so bad as this, still the prospects are not uniformly favourable, even if our purpose aims, not at the complete suppression of malaria, but only at checking the more severe endemic and epidemic manifestations. We have in that case to exterminate only *M. ludlowi*, *M. aconita*, *N. maculatus*, perhaps *S. aitkenii*, and in some places perhaps *N. leucosphyra* and *M. umbrosus*. It will simplify our task considerably, provided these species are restricted in their breeding-places, otherwise we may as well commence our operations against all local Anophelines, excepting only the breeding-places peculiar to *M. indefinita*, *C. kochii* and *N. punctulata* (*tesselata*).

This, unfortunately, is the attitude which we have to take with regard to *M. aconita* and *N. maculatus*. For reasons mentioned above, specific sanitation cannot be put into operation. Even if in a certain district, one of these species seems to be limited to one type of breeding-place, still we cannot advise the exclusive abolition of the larva, because observations from other localities have taught us that it may readily take to another kind of breeding ground. Nevertheless the study of the breeding habits of these mosquitoes has given us some useful knowledge. We have often observed careless cultivation of the rice-fields by the natives; the fields are inundated before being sown, in order to simplify the operation of ploughing; after harvesting, the water is not allowed to drain off, and, in consequence, the rice-fields are converted into swamps. Fields are frequently seen, in which the rice-stalks lie down in the water, because the owner of the field neglected to cut the ears in time. Such rice-fields constitute favourable breeding places for many species of Anophelines, among them *M. aconita* and *N. maculatus*. This negligence is harmful, not only from the sanitary standpoint, but also for agricultural reasons, and the latter reason alone should help to bring about an improvement.

On the other hand, whenever the species occurs in well-cultivated rice-fields, nothing at present can be done to prevent its propagation.

The larval habitat of the "littoral" *M. ludlowi*, on the contrary, facilitates sanitary measures; also, the "inland" form may be exterminated by the abolition of fish-ponds. Without improvement in the methods of rice cultivation, however, little can be accomplished.

CONCLUSIONS.

1. The eradication of Anopheline larvae, in the Malay Archipelago, is difficult because they breed in all kinds of temporary collections of water, which constantly reappear throughout the rainy season.

2. Anti-larval measures directed against *M. aconita* and *N. maculatus* are hard to carry out; specific sanitation is rendered difficult by their breeding habits, but amelioration may be expected as the result of improved methods of rice cultivation.

3. Specific sanitation is practicable in malarious regions where *M. ludlowi* is the chief vector.

The observations detailed in this paper might lead to the supposition that, in the Malay Archipelago, our investigations have been more academic than practical. This is not so. In several places on the sea shore (Siboga, Belawan in Sumatra, Batavia, Tegal, Semarang, Soerabaia, Tjilatjap in Java), and in some localities of minor importance in the interior, anti-malarial operations are in progress, or in preparation, but years must elapse before we can appreciate their effect. Where a distinct amelioration has been observed (*e.g.* Siboga) we are uncertain as to whether this should not be attributed to a remission in the intensity of endemic malaria, so frequently observed in the Malay Archipelago. So soon as conclusions may be drawn regarding the efficacy of our sanitary measures, we hope to make them known.

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ON THE LIFE HISTORY OF *BUCENTES* (*SIPHONA*) *GENICULATA* (DIPTERA: TACHINIDAE), PARASITE OF *TIPULA PALUDOSA* (DIPTERA) AND OTHER SPECIES[1].

By JOHN RENNIE, D.Sc.

AND

CHRISTINA H. SUTHERLAND, M.A., B.Sc., Carnegie Scholar.

(*From the Laboratory of Parasitology, University of Aberdeen.*)

(With Plate XIV.)

The Dipterous Family, Tachinidae, comprises a very large number of species whose larvae live as parasites within other insects, particularly in their larval forms.

Bucentes (*Siphona*) *geniculata*, one of the Tachinidae whose larvae are considered in the following paper, is a small ordinary looking fly, blackish in colour and showing a somewhat greyish abdomen, with prominent abdominal bristles. The labium is long and slender, sharply geniculated about the middle of its length, and folded like a clasp knife under the head when not in use[2].

In a former paper (1912) one of us has recorded the occurrence of the larva of this species as a parasite in the body cavity of *Tipula* larvae. It is probably not confined to one host species. In one collection of *Tipula* larvae, a proportion of which yielded the parasite, the majority of the survivors, on hatching, proved to be *Tipula oleracea*. In most instances, however, we have found the infected insects to be *T. paludosa*.

Since the original observation in 1912, we have found this larva regularly every year, and consequently regard it as a normal parasite of *Tipula*. Other observers record it from *Mamestra brassicae* and a related species, *Siphona cristata*, is reported by Roubaud (1906) to occur in *Tipula gigantea*.

OCCURRENCE AND DISTRIBUTION OF THE ADULT FLY.

From an examination of records relating to the adult insect, kindly submitted to us by the entomologists in charge at the British Museum and the Royal Scottish Museum, we find the fly is widely distributed throughout

[1] This work has been carried out with the aid of Grants from the Board of Agriculture for Scotland, to whom we desire to express our thanks.

[2] A full description of the structure and habits of the adult fly is reserved for a further paper

Great Britain. It is recorded from Devon, Hereford, Hants, Kent, Radnor, Middlesex, Hampshire and Inverness-shire. We have found it in Northumberland and Aberdeenshire.

The adults of this fly are recorded over the period from May till September. Schiner (1862) writes regarding the genus: "The flies live in dry places especially heaths. They are also found on Umbelliferae and on waste ground are often to be seen in large crowds on *Daucus carota*." He also states that *B. geniculata* visits *Erica vulgaris*. Walker (1853) reports these flies as "very common."

The following list of flowers known to be visited by *B. geniculata* is compiled from Knuth's *Handbook of Flower Pollination* (1909).

Viola lutea.
Stellaria holostea.
Medicago lupulina.
Potentilla sylvestris.
Potentilla sterilis.
Daucus carota.
Hedera helix.
Asperula cynanchica.
Asperula odorata.
Valerianella olitoria.
Succisa pratensis.
Eupatoria cinnabinum.
Pulicaria dysenterica.
Myosotis sylvatica.
Mentha aquatica.
Origanum vulgare.
Hottonia palustris.

METHODS OF INVESTIGATION.

The Tipula larvae, after being washed free of soil, were examined individually and with a little practice the parasitic maggot could be readily recognised beneath the skin of the host larva as an elongated yellowish patch of definite shape.

The proportions found to be infected varied a good deal in different localities and in different years. In one area, viz. Echt, Aberdeenshire, the numbers reached a significantly high figure. Over a period of one month, during which larvae were examined, a progressive decrease in the percentage of infected individuals was noted. This was found to be due to the fact that as the season advanced, the infected larvae were dying off, and pupae of *Bucentes* were becoming increasingly more numerous in the soil. It must therefore be borne in mind that for the first generation, unless examinations are made not later than about February, any estimate of the degree of infection must be below that actually existing. The following data illustrate this:

LARVAE COLLECTED IN ECHT AND LOWER DEESIDE AREAS.

Data for 1918.

Lot	Date	Infected larvae	Healthy larvae	Total	Percentage infected
1.	Feb. 20	170	434	604	28·1
2.	„ 27	127	243	370	34·3
3.	„ 28	164	524	688	23·8
4.	Mar. 1	73	386	459	16·0
5.	„ 6	103	442	545	19·0
6.	„ 7	182	819	1001	18·2
7.	„ 11	56	345	401	13·7
8.	„ 16	42	258	300	14·0
9.	„ 23	79	221	300	26·3
	Totals	996	3672	4668	21·3

LARVAE COLLECTED IN NORTHUMBERLAND.

For purposes of comparison we obtained a lot of larvae from the north of England. These yielded the following result:

Date	Infected larvae	Healthy larvae	Total	Percentage infected
Mar. 1	51	794	845	6·0

In other areas where larvae were collected in fewer numbers, the parasite was also found and all our observations suggest that it is relatively abundant.

During the season 1919, *Tipula* larvae were again collected and further data concerning the occurrence of *Bucentes* parasites were obtained.

Search was made for *Tipula* larvae in fields on the College of Agriculture experimental farm at Craibstone, Aberdeenshire, from the month of December onwards. During December and January only very small numbers of *Tipula* larvae were found and of these none were infected with *Bucentes*. In February and March the numbers found increased slightly and out of 56 larvae, three were found infected, one of these harbouring four parasitic maggots.

From April onwards appreciable numbers were obtained; the data for the season are shown in the table given below:

LARVAE COLLECTED IN LOWER DEESIDE AND LOWER DONSIDE.

Data for 1919.

Lot	Date	Infected larvae	Healthy larvae	Total	Percentage infected
Craibstone.					
1.	April 7	25	349	374	6·6
2.	„ 11	39	237	276	14·1
3.	„ 22	56	429	485	11·5
4.	„ 25	46	288	334	13·4
5.	May 8	1	155	156	0·6

No infected larvae obtained here during period May 9 to June 20.

LARVAE COLLECTED IN LOWER DEESIDE AND LOWER DONSIDE (*continued*).

Data for 1919.

Lot	Date	Infected larvae	Healthy larvae	Total	Percentage infected
Craibstone.					
6.	June 21	13	66	79	16·45
7.	„ 25	23 (+7 otherwise infected)	30	60	38·6
8.	„ 30	22 (+6 otherwise infected)	49	77	28·5
9.	July 7	6	9	15	40·0
Anguston, Culter.					
10.	April 26	1158	3467	4625	25·0
11.	May 2	107	456	563	19·0
12.	„ 9	50	903	953	5·2
13.	„ 16	3	807	810	0·37
		1562	7245	8807	17·6

As is indicated in the foregoing table no infected larvae were obtained between May 16th and June 21st. This was the case in other areas in the north of Scotland of which several were examined.

The fall to 0·6 per cent. at the beginning of May, and the complete absence of infected larvae in the soil for nearly five weeks, we attribute to the fact that the *Bucentes* maggots had pupated, and thus the *Tipula* larvae then found were such as had escaped infection by the parasite.

Larvae obtained at Craibstone on June 21st showed an appreciable percentage infected by *Bucentes* larvae, and from that date until July 7th, when the oats had grown too high to allow of further search for grubs, infected larvae continued to be obtained in high percentages, as is shown in the table.

NUMBER OF PARASITIC LARVAE PER HOST.

Observations made in 1918 show that one, two, three, and even four parasitic maggots may occur in one host. This was also the case in specimens found in the early months of 1919. A noticeable feature among the larvae found in the later part of 1919, viz. from June 21st onwards, was that there were seldom fewer than two *Bucentes* maggots in each host larva, 5–6 being common, and in one case as many as nine *Bucentes* maggots were found in a single host.

SIZE OF PARASITIC LARVAE FOUND.

Larvae from 1·5 mm. up to 8·5 mm., which represents the maximum size, have been found.

Even within the same host, the larvae may differ in size. For example, two maggots, 5 mm. in length, were found in the same host along with two others of 3 mm. In one case, where nine parasites occurred together, these were all 3 mm. in length. It seems more probable to us that these differences

in size in parasites occurring together are due to variations in the rate of growth than that the same host should have been parasitised on two or more separate occasions.

DURATION OF LARVAL PERIOD.

First Generation. In the season 1918, *Bucentes* larvae were obtained as early as February 20th. These larvae were on an average about 4 or 5 mm. in length at this date. In 1919, these larvae were first obtained on February 28th; they were from 3 to 5 mm. in length. This suggests that the parasitic larvae found in February are the product of eggs laid the previous autumn, the larvae having hibernated in the host.

Second Generation. From June 21st onwards, large percentages of the collected host larvae were found to be infected with *Bucentes*, whose maggots were of such a size, viz. 1–3 mm., as to lead to the suspicion that the *Tipula* larvae had been recently infected. From these *Bucentes* maggots a second generation of flies was bred which began to emerge on July 25th. An earlier generation of flies was bred out in May and the early part of June and by June 13th all these flies had died. Moreover, from May 16th to June 16th *Tipula* larvae were collected on four different occasions, to the number of 355, and of these none were found to be infected by *Bucentes*. This evidently indicates that all the parasites had pupated, involving the death of the host larvae, so that the *Tipula* larvae collected between these dates were those which had escaped infection by *Bucentes* during the previous autumn. In view of the foregoing, viz. that there is a period of over four weeks during which no infected *Tipula* larvae can be found in the field, that within this period adult flies appear to die off and that subsequently infected larvae again appear, the conclusion seems obvious that a second generation of *B. geniculata* commences about this time.

Bucentes maggots of the second generation were observed on June 16th, when they measured about 3 mm. The earliest date on which mating was observed was June 2nd, and no imagines survived in the observation cage after June 13th. Oviposition, and the infection of *Tipula* larvae in the field, may therefore be assumed to take place approximately within a corresponding number of days. Pupation of the second generation of larvae was observed to begin in the experimental cage about July 8th. That is to say, the maximum extent of the larval period possible was in this case from June 3rd to July 8th, viz. five weeks. This estimate is only an approximate one, as oviposition has not been observed and the period which elapses between oviposition and the hatching of the larva is unknown.

We have been able to find in the literature dealing with this subject only the scantiest references to this species. Nielsen (1918), in a table showing the life cycle of a number of Tachinidae, includes *Bucentes geniculata* in the form reproduced below, wherein P. signifies Pupa, L. = Larva, I. = Imago.

	April—May	June	July	Aug.	Sept.	Oct.	Nov.—April
Bucentes geniculata	P.I	L.P.I.	I.	I.I.	I.I.	P.	P.

Unfortunately, there is no evidence in the paper regarding the locality to which the data relate, but it would appear that the species may exist in the pupal condition from October to April.

For comparative purposes we append our data, which show that we are familiar with the life cycle of the parasite during the period from February to August, and that our information would indicate that the winter is spent in the larval condition in our area. Both records agree in showing that two generations occur in the year—a short-lived summer and a longer winter generation.

	April—May	June	July	Aug.	Sept.	Oct.—Nov.	Feb.	March	April
Bucentes geniculata	P.I.	I.L.	L.P.I.	I.	?	?	?L.	L.	L.P.

Pupation.

Observations show that usually the maggot leaves the body of its host and pupation takes place outside in the soil. After having emerged from the host larva, the parasitic maggot may still remain attached, as described later, to the tracheal trunk of the host, but usually the separation from the host, preparatory to pupation, is complete. In one instance, however, pupation was observed to have taken place within the host larva—the latter being still alive.

Within twenty-four hours after the maggot leaves its host, pupation is complete.

Period of Pupation.

First generation. In the season 1918, pupation was first observed on April 1st. The earliest date on which *Bucentes* flies emerged was April 23rd, so that approximately pupation extends over a period of three weeks.

In the season 1919 puparia were first observed on April 24th and flies began to emerge on May 14th. In this instance, the duration of pupation was 20 days.

Second generation. From observations made on pupae obtained from larvae of the second generation in the season 1919, we found pupation to extend from July 8th to 25th, *i.e.* over a period of 17 days.

Emergence of Adults.

In 1918 adult *Bucentes* flies were seen in the observation cage as early as April 23rd. Emergence continued until June 4th, after which date all the flies had died off.

In 1919, when the weather was less favourable, no flies were seen until May 14th. By June 13th all the flies had died.

In 1918, emergence continued therefore over a period of about six weeks. The flies which issued in April were rather small, but those which emerged during May were normal in size.

In 1919, emergence of flies continued only for about four weeks. In the

case of the second generation which began to appear on July 25th, the period during which emergence took place was about three weeks.

In order to find out from what depths the adult fly could emerge, the following experiments were set up.

Glass cylinders were filled with earth; in one the soil was loose, in another the soil was moderately compact. Puparia were placed at various depths, these being indicated by strips of gummed paper at the same level on the glass cylinder.

It was found that in loose soil the adult fly emerged from puparia placed at a depth of 2 and 3 inches, but did not emerge from puparia placed 6 inches below the surface. In moderately compact soil, the adult fly emerged from puparia placed at a depth of 3 inches, but not from a depth of 6 inches. The puparium cases were afterwards found at the levels at which they were originally placed. It has been noted that the parasitic maggot, after leaving the dead host, is capable of moving about in the soil, and probably it moves upward near the surface before pupating.

MATING.

Mating took place freely in the cage; in 1918 from May 16th to the end of the month; in 1919, from June 2nd till about the 12th.

Mating *Bucentes* were isolated in a test-tube with one or two daisy blossoms and kept under observation. The flies were found to remain *in coitu* over a period of about two hours. Oviposition was not observed, but flies which had mated were found to survive 4–5 days.

During both seasons, 1918 and 1919, pairs of mating flies were isolated along with *Tipula* larvae, and also in view of their recorded occurrence in *Mamestra*, along with various caterpillars, *e.g. Agrotis exclamationis*. No infection took place under these conditions.

LONGEVITY OF THE IMAGO.

Experiments were carried out to ascertain longevity of adult *Bucentes*, wherein newly-emerged flies were isolated in glass cylinders. In the bottom of the cylinder was put about 2 inches of earth in which one or two flowering daisy plants were placed to provide food for the flies. Under these conditions the flies survived 5 to 10 days. Under natural conditions they doubtless live longer than 10 days.

The confined flies are strongly attracted to light, they are exceedingly active and run about freely upon the surface of the soil. This was planted with daisies and dandelions, which were much sought, the flies being seen to introduce their proboscides into the daisy florets and to feed on the pollen.

SUMMARY OF LIFE HISTORY.

So far as we have been able to trace the life history of *Bucentes geniculata* it may be summarised as follows:

The winter months are spent as larvae within their hosts. viz. *Tipula* larvae. Pupation may start as early as the beginning of April if the season is good but in a late season, pupation may not begin until nearly the end of this month. After a pupal period of about three weeks the imagines emerge during April and May. By the middle of June the adult *Bucentes* are dying off. A second generation appears in June. After a larval period of about three weeks and a pupal period of about seventeen days the adult flies emerge towards the end of July. Since *Tipula* larvae are found in the winter months parasitised with *Bucentes*, infection probably takes place in the autumn whilst the *Tipula* larvae are comparatively young[1].

Structural relations of the Parasitic Larva to its Host.

Dufour (1827) described the larva of the Tachinid *Ocyptera bicolor*, which inhabits the body cavity of an Hemipteron, *Pentatoma grisea* Latr. He observed a membranous funnel-like structure, equal to about one-third of the length of the larva, extending from the last segment of the body and adhering by means of a pair of horny teeth at the other end to a metathoracic stigma of its host. He noted that this "siphon" could be detached from the larva without injuring it and he also found in other cases, "siphons" adherent to the metathoracic stigmata of the *Pentatoma* in the absence of the parasitic larvae.

Kunkel d'Herculais (1879) described a similar structure in the larva of *Gymnosoma rotundatum* Linn., and regarded the siphon as a product of the larva. In a Tachinid larva of *Carabus*, Cholodkowsky (1884) found a similar structure fixed to a trachea and described it as a chitinous funnel. He interpreted this as a pathological chitinous product produced by the hypodermal layer of the trachea at the point where the larva, having entered by a stigma, perforated the tracheal system to reach the body cavity.

Pantel (1898 and 1909), in *Thrixion Halidayanum*, clearly established the true nature of this funnel as an inflammatory reaction on the part of the host, and has more particularly shown how these anatomical relations are established between the host and parasite by a development of the hypodermal cells of the skin or of the trachea, whichever structure was utilised by the larva as a means of bringing its stigmata into direct relation with the external air. The perforation of the host's tissue at the point where attachment eventually takes place is effected primarily by means of the hooklets or spines which surround the stigmatic area of the parasite.

Roubaud (1906) describes the relations between *Siphona cristata* and its host, *Tipula gigantea*, in the following terms:

"A ce stade relativement jeune, chaque parasite est encore complètement inclus dans un kyste fermé, membraneux, fixé au cordon trachéen par une sorte de calice chitineux dont le fond s'ouvre dans la trachée chez les larves

[1] The summary of the life history as given by Nielsen, is quoted on p. 203

plus âgées, en croissance active, le kyste, détruit antérieurement, n'abrite plus que la région postérieure; le calice chitineux devenu plus épais emboîte étroitement l'extrémité postanale du parasite, allongée en un court siphon respiratoire bisegmenté.... La structure histologique de ces organes permet en effet d'affirmer leur nature trachéenne. A la base, les cellules hypodermiques sont abondamment développées et en plusieurs couches. La sécrétion chitineuse ne forme plus, par suite, un simple filament spiral, mais une couche continue, épaisse et noire, de chitine: c'est cette région qui constitue proprement le calice. Antérieurement, l'épaisseur de la paroi kystale s'atténue, comme par étirement de la formation précédente, jusqu'à se réduire à une mince couche chitineuse incolore où l'on ne distingue plus que quelques ilots de cellules hypodermiques, les débris de mues s'ajoutent à l'ensemble."

In *Bucentes geniculata* we have found structural relations between host and parasite similar to those cited above (Pl. XIV, figs. 1, 3, 4, 5, 6, 7 and 8).

The larva of *B. geniculata* lives in the body cavity of *Tipula paludosa*. We have not, so far, found it free in this situation, but always attached to one of the main tracheal trunks of its host by means of a chitinous sheath-like structure similar to that described by the observers quoted.

At its junction with the trachea of the host, and for a short distance along its length, this sheath is thicker and of a dark brown colour. Beyond this, it is membranous in appearance and completely encloses the parasite. Usually, however, and more particularly in the older larvae, the head end of the parasite is extruded from the sheath freely into the body cavity of the host.

Recalling Pantel's description and figures of the genesis of the funnel, in which he shows that the hooks at the posterior end of the parasite are utilised to perforate the skin of the host, it seems probable to us that the attachment between parasite and the tracheal system is established in a similar manner in *Bucentes geniculata*. The body spines of the first-stage larva appear well suited for such a purpose. At first the hind end of the parasite is adherent to the host at the place where the inflammatory reaction is developed, and its skin becomes incorporated with the funnel. On moulting taking place, the larva leaves this portion of its cuticle and retracts away, leaving a clear space in this area. The relation thus set up between parasite and host involves the perforation of the host's tracheal system and establishes a common respiratory system for both. Within the sheath there are always to be found the mouth-parts and spiracles of the previous moults. In this way we have obtained from third-stage larvae two sets of moulted mouth-parts and both anterior and posterior spiracles.

DESCRIPTION OF LARVA.

First-stage Larva. As in almost all Cyclorraphous Diptera, the larva passes through three stages separated by two moults. *The first-stage larvae* obtained measured about 1·5 mm. Thirteen segments could be distinguished. The head, as is usual in Cyclorraphous Diptera, is divided anteriorly by

a deep median groove into two lateral lobes each of which bears a rudimentary bell-shaped antenna.

All the segments bear black chitinous hooks with the points directed backward. On the cephalic and prothoracic segments are several series of hooks, but on the remaining segments, these are smaller and fewer in number. Each of the intersegmental grooves of the abdomen is margined by hooks whose points are oppositely directed on each side of the groove.

The larva is metapneustic at this stage, the post-abdominal spiracles being terminal. These communicate with two lateral tracheal trunks.

The mouth-parts differ considerably from those of the later stages. The cephalo-pharyngeal sclerite is strongly chitinised, its posterior margin being deeply embayed. Anteriorly it is prolonged as a slender bar and terminates in a wedge-shaped vertical plate which protrudes from the mouth. Ventro-posteriorly to this terminal wedge, there lies a free sclerite which is probably homologous with the dentate sclerite of the second and third stage larvae (Pl. XIV, fig. 10).

The Second-stage larva is about 3 mm. long (fig. 3). All the segments bear small chitinous hooks, so directed that each intersegmental area is bounded by two sets of hooks, one set pointing backward, the other forward. These hooks are few in number, each segment bearing only one or two rows. Besides these all the segments bear several series of blunt transparent spines.

The prothoracic spiracles (fig. 25) terminate in five or six papillae. The post-abdominal spiracles are borne on two tubercles, each having three clefts surrounded by peritremes. On the outer border of each peritreme lies a white spot, the opening of the perispiracular gland (figs. 18 and 19).

The bucco-pharyngeal apparatus is similar to that of the third-stage larva but only half the size (fig. 11).

Third-stage Larva. The full-grown larva, when ready to pupate, is about 8·5 mm. long and 1·75 mm. in diameter. There are two cephalic segments, the first bearing rudimentary bell-shaped antennae while the second on its ventral surface bears a patch of backward pointing chitinous hooks. Behind the cephalic segments, eleven segments can be distinguished. Of these three are probably thoracic and eight abdominal. On the ventral surface these segments bear two series of similar hooks, one on the anterior margin pointing backwards, the other on the posterior margin pointing forwards. Each intersegmental groove is therefore bounded by two series of hooks pointing in opposite directions. These hooks are of two kinds—small, sharp and chitinous, and large, blunt and transparent. The small chitinous hooks are borne on the second cephalic segment and on the last three abdominal segments where they are directed forward (fig. 4).

The tracheal system consists of two longitudinal trunks, united posteriorly by a commissure, having along their length branching lateral tracheae.

The prothoracic spiracles, which emerge on the anterior margin of the first thoracic segment, are fan-shaped with from six to eight lobes. In some

cases the prothoracic spiracles show a different number of lobes in the same larva, *e.g.* one spiracle has seven, the other eight lobes (figs. 20–24).

The post-abdominal spiracles are borne on two tubercles arising from the terminal segment. These tubercles are surrounded by a chitinous hoop which is open and flattened on the inner side. Each tubercle is again bilobed, each secondary lobe opening to the exterior by two slits. Thus within the chitinous hoop there lie four slits. These slits are surrounded by oval peritremes whose internal border is dentate. The peritremes lie so that their axes converge towards the inner border of the collar. The spiracle tubercle shows two white spots, the openings of perispiracular glands (fig. 17).

The spiracles communicate with the tracheal trunks through a "felt-chamber" which is a short tube filled with a spongy chitinous structure.

On the ventral surface of the last abdominal segment lies the anus in the form of a cleft with a protuberance on each side. The posterior end of the larva moves freely in the chitinous funnel, and, as far as has been observed, the post-abdominal spiracles are never closely adpressed to the host trachea but the air from the host trachea is drawn into the chamber formed by the adhering chitinous funnel where it is at the disposal of the larva.

Bucco-Pharyngeal Apparatus.

The complete masticating apparatus of the mature larva of *Bucentes geniculata* consists of a number of paired sclerites, the members of each side articulating with one another to form a united whole (figs. 12 and 13).

Overhanging the oral aperture is a pair of strong curved hooks, the *mandibular sclerites*. Dorso-posteriorly these have a dentate process, while ventro-laterally they bear a blunt wedge-shaped process. A ventral view shows the mandibular sclerites to be united by a cross bar. Each ventro-lateral process is perforated by a minute pore.

Articulating with the posterior border of the mandibular sclerites are the *hypostomal* sclerites which are united ventrally by a transverse bar. Between the mandibular and hypostomal sclerites there lies ventrally a fused dentate sclerite which is perforate.

The posterior extremities of the hypostomal sclerites articulate one on each side with the *cephalo-pharyngeal sclerites*, which have each a slight anterior rectangular prolongation, joining it to the hypostomal sclerite of its side. The cephalo-pharyngeal sclerites are prolonged dorsally, into wing-like processes which are perforate near their outer edges, and ventrally, into a stout somewhat rectangular posterior process which has a curved incision at its extremity.

The cephalo-pharyngeal sclerites articulate ventrally with a broad chitinous plate, the floor of the pharynx, as do also the extremities of the posterior ventral processes.

The Puparium (fig. 14). The puparium is brown in colour, barrel-shaped and with clearly marked segments. Each segment bears a double series of

hooks, one series pointing backward, the other forward. The rounded contour of the first segment is broken by the slightly projecting anterior spiracles, which are directed laterally outward. Posteriorly the puparium narrows distinctly into a short tubular portion which terminates in two bifurcated lobes, the post-abdominal spiracles. In the intersegmental space which separates the first and second abdominal segments are a pair of holes situated on the latero-dorsal side.

In a future paper we hope to deal with certain gaps in the foregoing account of the life history and to give a description of the structure and habits of the adult fly.

ACKNOWLEDGMENT.

We desire specially to express our thanks to Dr D. Keilin, of the Quick Laboratory, who has generously placed his extensive knowledge of the literature at our disposal, and also been most helpful with friendly criticism and suggestions. We have further found his recent work on the life-history and larval anatomy of *Melinda cognata* Meigen, parasitic in the snail *Helicella* (1919), of much assistance in determining the morphological details of the various larval stages.

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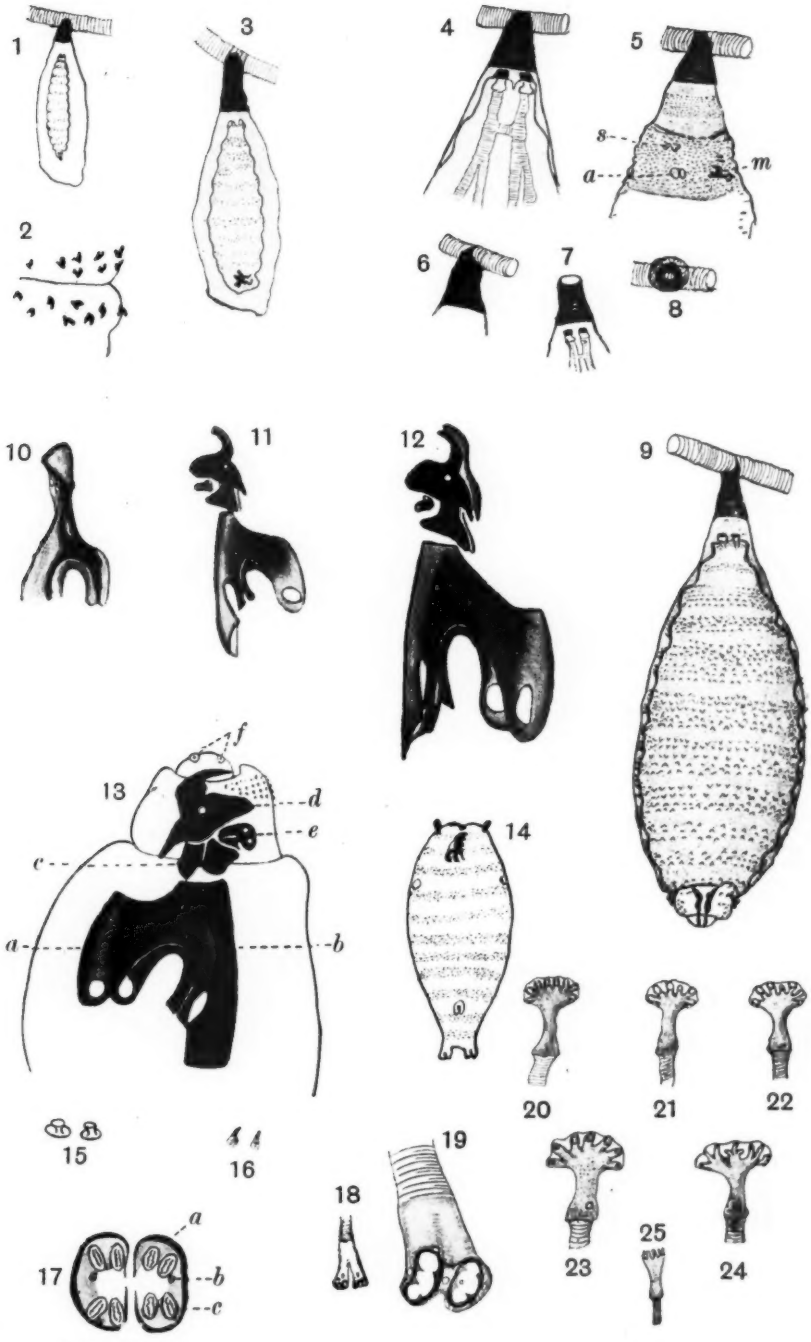

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EXPLANATION OF PLATE XIV.

Fig. 1. First-stage larva within the sheath.

Fig. 2. Intersegmental area of first-stage larva showing spines.

Fig. 3. Second-stage larva within the sheath.

Figs. 4, 5, 6, 7 and 8. Different views of attachment of larva of *B. geniculata* to its host; Fig. 5 shows the terminal part of sheath containing moult of second larval stage. The post-abdominal spiracles (*s.*) and buccal apparatus (*m.*) of the second-stage larva can readily be made out; fig. 7 shows the sheath detached from the trachea, and fig. 8 shows the attachment to trachea (end view).

Fig. 9. Third-stage larva showing anterior end protruding from sheath.

Fig. 10. Bucco-pharyngeal apparatus of *B. geniculata*, first-stage larva.

Fig. 11. Bucco-pharyngeal apparatus of second-stage larva.

Fig. 12. Bucco-pharyngeal apparatus of third-stage larva.

Fig. 13. Head and bucco-pharyngeal apparatus of third-stage larva; *a.* dorsal process; *b.* cephalo-pharyngeal sclerite; *c.* hypostomal sclerite; *d.* mandibular sclerite; *e.* dentate sclerite; *f.* rudimentary antennae.

Fig. 14. Puparium.

Fig. 15. Rudimentary antennae.

Fig. 16. Chitinous segmental hooks of third-stage larva.

Fig. 17. Post-abdominal spiracles of third-stage larva; *a.* chitinous hoop; *b.* opening of peri-spiracular gland; *c.* peritreme.

Figs. 18 and 19. Post-abdominal spiracles of second-stage larva, showing three peritremes.

Figs. 20–24. Prothoracic spiracles of third-stage larva.

Fig. 25. Prothoracic spiracle of second-stage larva.

A SURVEY OF CAWSTON'S SPECIES OF SOUTH AFRICAN CERCARIAE.

By ERNEST CARROLL FAUST, Ph.D.,

Parasitologist, Union Medical College, Peking, China.

(*From the Department of Pathology, Union Medical College, Peking.*)

(With 4 Text-figures.)

For several years Dr F. G. Cawston of Durban, Natal, has been making examinations of various mollusks taken from the rivers and pools of the Transvaal and Natal in order to discover the fluke infection of the region. These examinations have been extensive as regards the number of individuals of each species examined, ranging up into the thousands for the more common gasteropods. The investigations have been carried on through the various seasons of the year so that the data are representative. I have been enabled to re-examine much of this material through the courtesy of Dr Cawston, who has also placed at my disposal many of the biological data concerned with these researches.

It is common knowledge that the mollusk is the obligatory host of the larval fluke; that in regions where the geological or biological conditions are unfavourable for molluscan life trematodes do not occur; and that one usually expects to find fluke infection where molluscan life is abundant. But while the presence of the mollusk is an essential factor in the distribution of fluke diseases, it does not always follow that an abundance of trematodes follows an abundance of mollusks. Thus in certain parts of Japan and in the Yangtse Valley, China, fluke infection of man and other animals is common. Yet in North China, where the sanitary conditions are equally bad, trematodes are relatively rare.

Taken as a whole, one is impressed with the large number of individuals of such species as *Lymnaea natalensis* and *Physopsis africana* which Dr Cawston has examined. Infection is heavy in April and decreases toward July as the cold season comes on. Infection of *L. natalensis* is relatively light in the Transvaal and heavy at Durban. The number of infected individuals of *P. africana* is moderately few in both Natal and across the Vaal. Linked up with this fact is the paradoxical one that *P. africana* is infected with the highest number of species of cercariae (nine) and is the only host known for six of these species. *L. natalensis* has the next highest number of species (six)

of which three are specific. *Planorbis pfefferi* from Durban has a high infection which continues into the summer.

In all, 15 valid species may be recognised from the data in the writer's hand. Three of these have been recorded from the Transvaal alone, nine have been found solely in Natal, while three species are common to both regions. The larva of *Schistosoma haematobium* is apparently ubiquitous, having been recorded from Rustenburg, Pietermaritzburg, Magaliesburg, Mulder's Drift, Nijlstroom, Durban, and along the coast north of Durban.

Of these species the largest group is that of the furcocercous cercariae, containing the two human parasites, cercariae of *Schistosoma haematobium* and of *S. mansoni*. The second largest group, that of echinostome larvae, has no species that is now known to infect man in that region of the world. Either of the remaining species or others yet undescribed may be correlated with the adult liver flukes of sheep, and with monostome and amphistome infection in cattle in South Africa.

The life history of the schistosome is comparatively simple, as Leiper (1915), Manson-Bahr and Fairley (1920) and others have conclusively shown. The larva passes directly from the mollusk to the definitive host. Gilchrist (1918) has likewise shown that *Cercaria comma* is genetically related to *Distoma luteum* Gilchrist which is found in the frog. But analogy from life histories of some of the other groups leads one to believe that the solution of the problem in every case is not so simple, and that a second intermediate host may be expected.

A synoptic table of the valid species collected by Dr Cawston in the course of his examinations, together with the record of Gilchrist (1918), is included in this paper.

Material which the writer has recently had an opportunity to examine permits a description of *Cercaria pigmentosa* Cawston, previously inadequately described, and a new species of echinostome larva, *Cercaria* 30-*acanthostoma*, previously confused, perhaps, with *Cercaria catenata* Cawston, 1917.

Cercaria pigmentosa Cawston 1919.

HOST: *Lymnaea natalensis.*

HABITAT: Natal.

This species of cercaria is the first larva of its kind to be described from Cawston's material (Fig. 1). The body is distinctly cordate with the apex directed forward. The head region is slightly protruded from the rest of the body. The body measures $333\mu \times 281\mu$. The tail is about two and one-half times the length of the body when fully extended and has a proximal diameter under these conditions of 56μ. Both body and tail are entirely covered with minute spines. The mouth is ventral in position. It has a diameter of 50μ. It leads almost directly into a small oesophagus surrounded by a small but powerful sphincter. Behind this organ the digestive tract forks to form two

stubby limbs which reach to the subdistal region of the body. The acetabulum lies in the middle third of the body. It measures 43μ in diameter and is very muscular.

The excretory bladder is a conspicuous non-muscular organ with cornua extending forward and a median vessel running backward into the distal region of the tail.

The conspicuous flocculent masses from which the larva derives its name are not pigment masses at all, but dense creamy semi-opaque vitelline follicles which with the most careful treatment remain unstained. Near their posterior limits they are connected with the medially lying germ glands by a pair of transverse vitelline ducts. The germ masses are found to contain evidences of ovary, receptaculum, Laurer's canal, vagina and seminal ducts.

The redia in which the cercaria develops is a large sacculate body with a pair of so-called feet near the posterior end and a distinct collar anteriorly. The oral sphincter is extremely small. The redia is covered with minute spines.

The cercaria is provided with abundant material for encystment. The transfer to the subsequent host probably occurs after the fluke emigrates from the mollusk.

Cercaria 30-acanthostoma nov. spec.

HOST: *Physopsis africana.*

HABITAT: Lyndenham, Natal.

This cercaria is the fourth echinostome of Cawston's collection to be described. It differs markedly from *Cercaria arcuata* and *C. constricta*. While it more nearly resembles *C. catenata* it differs from that species in many significant points.

Cercaria 30-*acanthostoma* measures 300μ × 130μ. The tail is slightly longer than the body. It measures 41μ at the base and tapers gradually toward the tip. The body but not the tail is covered with flat rhomboid scales closely appressed to the integument (Fig. 4). There is a circlet of 30 collar spines with blunt points and bases deeply inserted in the integument (Fig. 3). The oral sucker is inclined ventrad. It measures 38μ in diameter. The acetabulum, which lies behind the middle of the body, measures 45μ by 54μ. Between the oral sucker and the pharynx is a slight prepharyngeal sphincter. Behind the pharynx is a long oesophagus which normally forks just in front of the acetabulum. The coeca reach to the subdistal region of the body, as in most echinostome larvae.

The excretory bladder is large and distended. The pore opens posteriorly. A median cornu connects the bladder with the main collecting tubules. The latter are somewhat convoluted (Fig. 2). They contain no excretory granules. Running backward from the bladder is the main collecting tubule for the tail. It bifurcates at the beginning of the distal fourth of that organ each fork of which opens externally. This caudal canal corresponds somewhat to the similar organ in *C. catenata*.

DISCUSSION.

With the larval stages of the more common species of flukes established for this portion of South Africa, the next problem in hand involves the discovery of the adult flukes in the same locality, flukes which possess gross

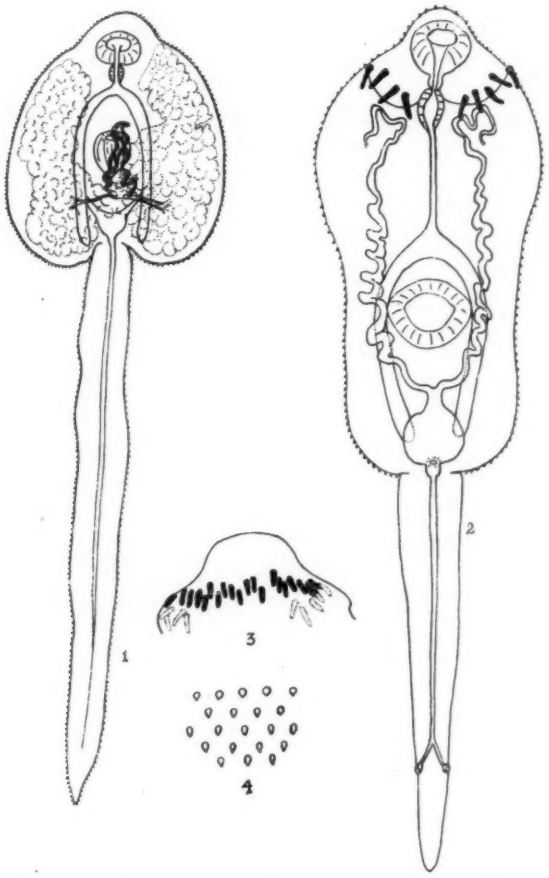


Fig. 1. Ventral view of *Cercaria pigmentosa*, showing digestive and reproductive systems. ×57.
Fig. 2. Ventral view of *Cercaria* 30-*acanthostoma*, showing digestive and excretory systems. ×115.
Fig. 3. Dorsal view of collar spines of *Cercaria* 30-*acanthostoma*. ×115.
Fig. 4. Integumentary spines of *Cercaria* 30-*acanthostoma*. ×242.

characters showing likely correlation with these larvae. It must be held in mind continually that many of the larval organs are *larval only* and disappear with metamorphosis; likewise, that some of the adult structures are not

recognisable in the larva. There are other characters, however, which are phylogenetically constant. These may be depended on in demonstrating the correlation.

It is not within the province of this paper to detail these fundamental homologous characters. However, the writer does desire to urge that these morphological characters be used hand in hand with the experimental work in investigating life histories, for neither one nor the other may be used alone without the danger of misinterpretation.

Table giving important biological data on South African Cercariae.

Group	Species	Described by	Date	Host	Locality
Amphistome	*C. frondosa*	Cawston	1918	*Isidora schakoi*	Potchefstroom
				Isidora schakoi	Stellenbosch
Monostome	*C. fulvoculata*	Cawston	1919	*Lymnaea natalensis*	Durban
Distome					
Echinostome	*C. catenata*	Cawston	1917	*Lymnaea natalensis*	Magaliesburg
				Lymnaea natalensis	Durban
				Planorbis pfefferi	Durban
				Physopsis africana	Durban
	C. arcuata	Cawston	1918	*Isidora schakoi*	Klerksdorp
				Lymnaea natalensis	Durban
	C. constricta	Faust	1919	*Physopsis africana*	Durban
	C. coma	Gilchrist	1918	*Isidora tropica*	Muizenburg Lake
	C. 30-acanthostoma	Faust	1920	*Physopsis africana*	Lyndenham
Xiphidio-cercariae	*C. cawstoni*	Faust	1919	*Physopsis africana*	Maritzburg
				Lymnaea natalensis	Maritzburg
				Planorbis pfefferi	Durban
Leptocercariae	*C. pigmentosa*	Cawston	1919	*Lymnaea natalensis*	Natal
Furcocercariae	*C.* of *Schistosoma haematobium*	Cawston	1915	*Physopsis africana*	Rustenburg
					Maritzburg
					Magaliesburg
					Mulder's Drift
					Nijlstroom
					Durban
					Ottawa
					Lyndenham
	C. of *Schistosoma mansoni*	Faust	1920	*Physopsis africana*	Durban
					Ottawa
					Lyndenham
	C. gladii	Cawston	1918	*Isidora schakoi*	Potchefstroom
	C. secobii sp. inq.	Cawston	1915	*Physopsis africana*	Maritzburg
	C. oculata	Cawston	1917	*Physopsis africana*	Durban
	C. parvoculata	Cawston	1919	*Physopsis africana*	Durban
	C. bilharziellalunata	synonym of *C. oculata*			
	C. spinosa, *C. crispa*	synonyms of cercariae of human schistosome species			

OBSERVATIONS ON THE GEOGRAPHICAL AND ETHNOLOGICAL DISTRIBUTION OF HOOKWORMS[1].

By SAMUEL T. DARLING,

Professor of Hygiene, Faculdade de Medicina e Cirurgia de São Paulo, Brazil.

During the course of investigations, primarily directed to a study of the effects of hookworm infection on people in different parts of the tropics, I have been struck with the peculiar geographical and racial distribution of the two common species of hookworms infecting man, and with its bearing on certain ethnological problems.

The observations I have made, in so far as they are related to anthropological questions, are as follows: The races of mankind, living in tropical and subtropical regions, are infested with one or more species of hookworms. In the migrations of these peoples the immigrants have carried their peculiar species of hookworms into regions occupied by people having a different worm-species-content, and by an examination of the intestinal worms of a people, the geographical and ethnic origin of their hosts can, within certain limits, be divined. I refer particularly to migrations within 35° N. and 30° S. latitudes, for when migrations are made into colder climates the hookworm infection is ultimately lost through inability of the embryos to persist during the phase of their life cycle spent in the soil.

There exists the deepest ignorance in regard to the migrations of people that have taken place in prehistoric times and also in regard to those within historic times where no records have been left.

But at present, in tropical countries, certain movements of populations are going on in response to a demand for agricultural labourers.

Large numbers of Tamils and Malabaris have been recruited to Malaya to work on rubber estates. Thousands of Chinese go annually to the same country to work in the tin mines. A great many North Indians from Calcutta are being employed under indenture in Fiji and British Guiana on cane and rice plantations, there is a Javanese colony in Dutch Guiana. Japanese are colonizing in the State of São Paulo, Brazil.

The origin and movements of these people are well known. They have brought enormous numbers of hookworms into the countries where they are employed. A study of the worms expelled from these people as well as those

[1] This work for the most part was done under the auspices of the British Colonial Office and with the support of the Rockefeller Foundation.

expelled from the autochthones in the countries in question discloses some interesting facts.

Taking the island of Viti Levu, the autochthones show almost a pure infection with one species of worm, *Necator americanus*. No specimens of *Agchylostoma duodenale* were encountered in Fijians except among those that had lived in towns, or near plantations occupied by East Indians.

Among indentured East Indian coolies from Calcutta 21·4 % of the worms expelled were *A. duodenale*, the rest were *N. americanus*.

Wherever Fijians were living near East Indians, they were found to have become infected with *A. duodenale*, derived from the latter race.

Infection by *A. duodenale* is becoming widespread among town-dwelling Fijians.

After East Indians have lived in Fiji for 10 to 15 years or more they lose a good many of their *A. duodenale* and disclose a relatively larger proportion of *N. americanus*.

In Malaya the Malays were found to harbour nearly a pure culture of *N. americanus*, for 98·99 % of their worms were of this species, the remainder being *A. duodenale* and *A. ceylanicum*. This may be considered the formula of the country. Chinese coolies coming in to Malaya bring a worm formula of 35 to 85 % *A. duodenale*, the remainder being *N. americanus*. However, among the generation of Chinese born in Malaya—Straits born Chinese, who have often taken up Malay customs—eating with their fingers, etc., and who may have dropped Chinese customs and associates to a greater or less extent, it was remarkable to find that they had dropped also the Chinese worm formula as well, and taken up one like that of the people of the country. At the same time the influx of Chinese coolies with their large ancylostome index is gradually adding an increasing number of hookworms of this species to the common species of the natives of the peninsula.

The effect of migration into a country whose people have a different index from that of the immigrants, is to make the immigrant take on the worm index of the autochthones, while the index of the latter is more or less modified by the implantation of the worm species of the immigrant.

This was very clearly shown in Fiji.

The autochthonous population as represented by the people of Nasoqo, a remote and inaccessible interior mountain village, were found to be infected with *N. americanus* (six specimens of *A. ceylanicum* were encountered). Not a single specimen of *A. duodenale* was taken. The ancylostome index of the autochthones then must be considered as nil.

In the villages near Nausori where the autochthones are exposed to infection from soil polluted by East Indians, they were found to be harbouring some *A. duodenale*. Thus ten Fijians treated, were found to have 1309 hookworms of which 1246 were *N. americanus* and 63 *A. duodenale* (there were six dog-worms *A. ceylanicum*).

The ancylostome index of these town-dwelling Fijians was 4·8 % and

represents infection derived from North Indian sources, for the ancylostome index of the Calcutta men was 27, while that of uncontaminated Fijians was nil.

Here we are to observe two tendencies. First: a tendency for the stranger to part with some of his worms and to acquire a worm formula like that of the natives. Second a tendency for the natives to acquire certain worms from the strangers and thus modify the primitive formula of the region or race. This is actually taking place in Malaya, Fiji, Guiana and Brazil. Changes analogous to these that are taking place under our very eyes, may be assumed to have taken place centuries ago among other peoples, and if among a people to-day whose worm formula is 99 % *Necator* we encounter a group who are harbouring 15 % *A. duodenale* or any notable number of that species we are entitled to assume that the hookworms of the latter people are derived from an alien stock.

The hookworms encountered in man are:

Agchylostoma duodenale.	*Necator americanus.*
,, *ceylanicum.*	
,, *braziliense.*	

These worms probably all have identical life cycles. *A. duodenale* and *N. americanus*[1] are obligate parasites for man, as they are not found in any of the animals.

A. ceylanicum and the less known *A. braziliense* are commonly found in dogs in certain tropical lands particularly in the Old World.

The adult sexually differentiated worms live in the small intestine and the females produce many ova which pass out in the faeces.

Embryos from the ova-infected faeces develop in the soil under suitable atmospheric conditions of warmth, moisture and oxygen.

The embryos penetrate the skin of the feet of people visiting polluted places and after traversing the skin, venous blood channels, right heart, lung and trachea, they reach the intestinal tract where they take up lodgement in the lumen of the small intestines, holding on to the mucous membrane by their strong armed mouths, and remaining in the host as long as seven or eight years.

While in general it has been recognized that two species chiefly were to be found in man, no survey has been made of the species actually harboured by the different races of mankind or by the inhabitants of different zones, regions or localities.

The reasons are obvious. Anti-hookworm campaigns are of very recent date and the doctor in charge is usually concerned merely in ridding the patient of worms and ameliorating his physical condition.

The washing of faeces after employing a vermicide, and the culling and counting of thousands of worms under field conditions is not an easy or enticing vocation.

[1] *Necator americanus* has been found in a gorilla by Leiper and Looss.

Rarely however it has happened that the careful counting of hookworms expelled from a large number of people was necessary to the elucidation of some intensely interesting and very important medical and public health problems. Such problems were presented to me and my colleagues, Doctors M. B. Barber, H. P. Hacker, M. B. Barnes and W. G. Smillie. In the prosecution of our work the drudgery of the task was alleviated by the extraordinary interest aroused as the solution of the problems appeared to present themselves.

DISTRIBUTION OF *AGCHYLOSTOMA DUODENALE.*

A. duodenale is distributed to all those countries lying in Eurasia, south of 35° N. latitude and north of 20° N. latitude. In Europe, as in Cornish mines and in Mediterranean countries and Egypt, it may be the sole species found; nearer the Tropic of Cancer it is associated with increasing numbers of *N. americanus*. In warm mines the worm may be found farther north than 35° N.

This species has been introduced into the American continent and the Antilles in historic times by coolies from India and Java, by Mediterranean and Levantine people into Brazil and other parts of North, Central and South America, and by Japanese and Chinese.

It has been introduced into Fiji by Indian coolies, and into Polynesia, the Philippines, and Australia, by Chinese, Japanese and Portuguese. In Europe it has been encountered in Italy, Sicily, Sardinia, Spain, Austria, Hungary, Serbia and Bulgaria. Farther north it is common among miners as in Cornwall, Belgium, Liège, Mons and Charleroi. In France it occurs in the Loire Basin, also in the mines of Germany, Poland and Silesia. Severe infections are encountered in Egypt.

While in general the species *A. duodenale* is distributed in the cooler latitudes north of 20° N. latitude, there seems to be no reason other than the lack of opportunities for implantation, for its relative absence in equatorial regions.

Its absence is only relative for I encountered large numbers of this species in Java and Malaya among people who acquired the infection within 3° N. and 8° S. latitudes. It is evident therefore that there is nothing in an equatorial climate inimical to the development of the species in the soil and that the incidence of each species is purely a matter of implantation on soil equally favourable to each.

DISTRIBUTION OF *NECATOR AMERICANUS.*

This species is found in largest proportion in Eurasia, Africa, Indonesia and Polynesia, south of 20° N. latitude.

In regions near the tropic of Cancer it is associated with *A. duodenale* but farther south, as in parts of Indonesia, Fiji and South Africa, it is encountered alone.

This species has been introduced into America within historic times by Kaffir slaves from Africa and to a certain extent by the East Indian coolies from British India and Java. It is the species most commonly found in America and has been spread from Virginia to Argentina.

It is possible that either or both species have also been introduced into the American Continent from Asia, Indonesia or Polynesia by voyagers or storm-tossed fishermen. This is an enticing subject for future research.

The American Continent may have been peopled (*a*) from Asia by way of Behring Straits, (*b*) from Asia or Indonesia across the Pacific, or (*c*)[1] from Polynesia across the Pacific.

In the case of (*a*) cold would prevent the continuance of infection and the migrants would arrive free from hookworm, unless of course the average temperature of the Straits during migration was equal to that of North Carolina at the present time, for the latter temperature is the northern limit of autochthonous hookworm infection in America. In the case of (*b*) we might expect to find either or both *A. duodenale* and *N. americanus* among the Amerinds or in such representatives of them as may have descended from (*b*). In the case of (*c*) we would expect to find only *N. americanus*.

A survey of the species of hookworms harboured by Amerinds unexposed to infection from other sources, is urgently required to clear up some of these points.

In Panama the population composed of Meztizos and Zambos was found to be almost exclusively infested with *N. americanus* which may have been derived in the first instance from Negroes.

The reports of the Field Director of the International Health Board working in Central America show that the Indian (Amerind) population is infested with hookworms but the observations have been carried out in localities and among Indians who have been living in an environment contaminated with excreta of Negroes and East Indians which contain embryos of both *Necator* and *Agchylostoma*.

It will be necessary to search for tribes in inaccessible and remote places when it is desired to ascertain the primitive worm species index of uncontaminated Indians (Amerinds).

GEOGRAPHICAL AND RACIAL DISTRIBUTION OF HOOKWORMS.

AMERICA.

The species of hookworms encountered in the Southern States according to Dr Stiles is *N. americanus*, this was derived no doubt from the introduction of negro slaves from Africa.

[1] Cowan (1910), *The Maoris of New Zealand*, Christchurch, N.Z., records that in 1909 a Chinese fishing junk picked up off the island of Chu San a party of three South Sea Islanders who were adrift in a canoe, they had mother of-pearl shell fish-hooks and other South Sea fishing tackle with them, and had been blown and drifted fully 2000 miles from a German possession in the Western Pacific.

No survey of the hookworms of North American Indians has yet been made. It is extremely important that this be undertaken without delay.

Panama.

In Panama there were two types of infection: (*a*) pure infections of *N. americanus* encountered among the Panamans and probably derived from African negro sources, (*b*) mixed infections in which both *A. duodenale* and *N. americanus* were found. This type of infection occurred chiefly among West Indians who had been exposed to infection in their native islands from East Indian coolie sources. But it also occurred to a slight extent among natives of Panama who had been exposed to infection from West Indian negroes resident in the Canal Zone since the commencement of canal operations.

Brazil. *State of São Paulo.*

The species most commonly found is *N. americanus* but the proportion of *Agchylostoma* to *Necator* varies in different communities depending on circumstances.

At *Itatiaia*, in a former coffee plantation where many African negro slaves were worked years ago, the ancylostome index is 1·5.

At *Rezende*, which was formerly a detention and distribution centre for Italian, Portuguese and Spanish agricultural colonists, the ancylostome index as we might expect is much higher, 11·2, and is evidently due to the seeding of the soil with *A. duodenale* by Mediterranean people.

At *Brodowski* the high ancylostome index of the Japanese is being markedly altered by residence among the native Brazilian agriculturists who are so heavily infested with *N. americanus*.

Nothing has as yet been done to determine the species formula of the aborigines of South America.

Great care must be exercised in selecting tribes who live in inaccessible regions unvisited by foreigners. It should not be hard to do this in the interior of the continent or in Andean villages.

Europe.

The species encountered in Europe is *A. duodenale* except in those immigrants returned from Brazil or the United States.

The hookworm found infecting Cornish miners was *A. duodenale* (Boycott).

Isola (1904) examined 11,000 specimens collected by Parona from upper Italy and all were *A. duodenale*.

Africa.

Northern Africa.

The species found in Egypt and Northern Africa appears to be exclusively *A. duodenale* for this was the sole species encountered in the large mass of material passed under review by Looss in Egypt.

Equatorial and South Africa.

In a number of autopsies I performed in Johannesburg on Kaffirs from Mozambique, the only species encountered was *N. americanus*.

Leiper, Looss and Fülleborn found this species in South Africa and among Pygmies in the Cameroons, respectively.

The Kaffirs[1] appear to be parasitized exclusively by this species. The introduction of slaves from Mozambique infested with *Necator* will account for the exclusive presence of this species in the Southern States of America.

ASIA—INDONESIA.

Malays. The natives of the Malay Peninsula.

The Malays live in kampongs or native villages usually occupied solely by individuals of their own race. This was particularly true of the two kampongs near Kuala Lumpur where we obtained some data.

Thirty-eight boys from Kampong Malacca yielded 2262 hookworms of which 2257 were *N. americanus*, and 5 were ancylostomes, 3 *A. duodenale* and 2 *A. ceylanicum*.

In Ulu Gombak 39 boys yielded 1559 hookworms, 1546 of these were *N. americanus* and 13 ancylostomes, of these 7 were *A. duodenale* and 6 *A. ceylanicum*.

Thus the percentage of ancylostomes present in the Malay kampong boys was 0·22 and 0·8 respectively.

Taking the two groups of 77 boys as a whole as representative of what the Malay worm formula should be and considering *Necator* and *A. duodenale* only, there were 3813 worms of which 10 only were *A. duodenale*, or an *A. duodenale* index or percentage of 0·26.

Adult Malays. Adults from their occupations are often brought into contact with Chinese of which there are large numbers in the peninsula and they have more opportunities for becoming infested with the hookworms of the Chinese, who, as it will be shown, harbour very large numbers of *A. duodenale*. We may expect the adult Malays to-day therefore to show some evidences of contamination from Chinese sources.

Sixteen adult Malays were found to harbour 1138 hookworms of which 10 were *A. duodenale* and the remainder *N. americanus*, the *A. duodenale* index being 0·9. Thus we see that the autochthonous Malay population of the Malay Peninsula harbours nearly a pure culture of *N. americanus*.

Malays of the Island of Java.

Among the natives of Java there was encountered a very distinct difference between the ancylostome index of the people of West Java and that of people

[1] *A. duodenale* unquestionably is a more malignant hookworm than *Necator*. It is possible that some of the alleged immunity of the negro to the effects of hookworm infection is due to the fact that Kaffirs and their descendants are very largely parasitized by *Necator* and not by *A. duodenale*.

living east of the Tji Manoek river, this difference corresponds with a difference in the ethnic stocks in the two regions.

Worm counts were carried out among Malays in four kampongs in the city of Batavia (West Java): a total of 2935 hookworms were obtained from 92 people of which only 26 were *A. duodenale*, the remainder being *N. americanus*; the percentage of ancylostomes therefore was 0·88 a figure corresponding closely with that of the Malays of the Malay Peninsula.

In the mountainous region of the Preanger (West Java) there was an absence of *A. duodenale* which was very striking indeed.

Twenty-five Malays (Sudanese) in the dessa or village of Endil Tjhoeavg-laagte were found to be harbouring 1275 hookworms, and of these two were *A. ceylanicum* (derived from dogs), the rest being *N. americanus*.

In the dessa of Tjimatjam, at an elevation of 3600 feet, near the volcano Gedeh, where there was a minimum pollution of soil and of the water courses, 25 persons yielded only 150 hookworms all *N. americanus*.

In these two dessas in the Preanger the *A. duodenale* index was nil.

This absence of *A. duodenale* among 50 representative Malays in the Preanger, indicates in the most striking way that the hookworm common and proper to the people of West Java is *N. americanus* and that *A. duodenale* when found represents an extraneous infestation from some alien source.

Wishing to include in the survey some of the people of mid-Java I visited two villages near Cheribon on the North Shore:

At Gebongelir, 50 Javanese were treated, and a total of 2339 hookworms were obtained from them; of these 308 were *A. duodenale* the remainder being *N. americanus*, the ancylostome index being 13·1.

At Kalimaro, a village near by, 5140 hookworms were obtained from 24 persons; 332 were *A. duodenale* and the remainder were *N. americanus*, an ancylostome index of 6·2.

In the dessa of Kebasekan near Keboemen, not far from Djokjakarta (mid-Java), 25 persons yielded 4082 hookworms, the percentage of *A. duodenale* being 5·4.

From Krakal and Karangsari, villages in the same district, 28 Javanese yielded 10,861 hookworms of which 770 were *A. duodenale*; the ancylostome index being 7·0 %.

The distribution of *A. duodenale* and *N. americanus* in Java and the neighbouring islands is well displayed in an analysis of the results of the worm findings among the prisoners in the jail in Batavia.

In this jail there are no opportunities for acquiring new hookworm infestation. Food is dispensed in a pasteurized or sterilized state while still warm. The sanitary arrangements while primitive I think effectually prevent hookworm infestation.

Confirmatory of this is the fact that of 118 men treated who had been in the jail for periods up to seven years or more, the average number per man was found to diminish with each succeeding year of imprisonment. This is inter-

preted as meaning that the older worms die and are expelled, while there is no re-infestation or new infestation to make up this loss.

The people living in the kampongs round about outside the prison have, as we have seen, an ancylostome index of 0·88 %.

Within the jail compound the index is 9·2 % from a total count of 8638 worms derived from 118 prisoners. This indicates that the prisoners bring their hookworms in with them and do not derive them directly or indirectly from the kampong people outside the jail through polluted water or food. We are confirmed in this view on an analysis of the findings, after separating the men into groups based on the part of the Netherlands Indies they came from.

Thus there were two prisoners giving their place of origin as Batavia or the Preanger, that is, West Java. The total worm count was 130 and the ancylostome index was 0·76 which is a West Java index.

There were nine prisoners from mid or East Java. The total worm count was 755 with an ancylostome index of 7·5 %—a mid-Java index.

Taking up the prisoners from Sumatra and other islands of the Netherlands Indies the index of each place may be ascertained from the prisoners and their respective differences noted.

Madura. This small island almost touches the eastern end of Java. There were 16 Madurese prisoners from whom 1263 hookworms were obtained; the ancylostome index was 13·7 %.

Bali. This interesting island, where the Hindu religious influence is still paramount, yielded five prisoners; the worm count was 348 and the ancylostome index 4·0 %.

Lombok, a neighbouring island, with 4 prisoners and a total worm count of 479, gave an ancylostome index of 3·3 %.

Timor. This island, with four prisoners and a worm count of 100, gave an ancylostome index of 62·0 %.

Sumatra supplied 12 prisoners. The total worm count was 919 of which only 7 worms were *A. duodenale*, the ancylostome index being 0·9 %. Thus the index of Sumatra resembles that of the people of the adjoining portion of West Java and the Malay Peninsula in contra-distinction to that of the people of mid and East Java and the chain of islands extending towards Timor.

(There were two prisoners who had worm formulas resembling that of the Chinese. One of these, a Madras Tamil, had lived five years close to Chinese lines. The ancylostome index of these two men (38 worms) was 65 %. It is evident that they were infested from Chinese sources.)

Celebes. This island lies to the north of Timor and to the west of Borneo.

It supplied four prisoners yielding 523 hookworms, all *N. americanus*, the ancylostome index therefore being nil and representing what we may call the primitive Malay species formula.

This completes the data, highly interesting and important as they are in respect to the indices of the autochthonous population of Indonesia.

Unfortunately there were no Malays from Borneo, Flores or Sumbava in our treatment groups, but the evidence as it stands, points distinctly to the supposition that the Malay people living in Sumatra (their ancient home?), Malay Peninsula, Java, Celebes and all the other islands of Indonesia were originally infested with *N. americanus* whilst *A. duodenale* became superimposed upon this infection in certain localities and islands through the migration thither of an alien ethnic stock or stocks infested with a much higher percentage of *A. duodenale* than that harboured by the autochthones.

From evidence to be presented there can be no doubt but that *A. duodenale* was introduced into Indonesia from the continent of Asia and in sufficiently large numbers to have become well implanted in the people and soil of mid and East Java and of Madura, Lombok, Timor and Bali as well.

What was the ethnic source of the migrants?

It was almost certainly from some region north of about 20° N. latitude and may have been North Indian, that is from above the delta of the Ganges or thereabouts, Upper Burmah or Assam or it may have been from China.

Regular commercial relations had been maintained between India and Java since about 700 B.C., according to Oldham[1]. Arab and Chinese merchants have been coming to Indonesia for centuries and from these three sources the soil of Indonesia undoubtedly has been seeded with *A. duodenale*.

But to account for the high ancylostome index encountered in mid and East Java, Madura, Lombok and Timor we must assume the migration of larger numbers than would be represented by a few traders and sailors.

A volume of people corresponding to the respective numbers of the two species of hookworms in the ancylostome index has been necessary to produce the index as we find it.

That is to say, a thousand migrants with an ancylostome index of 75 % when mixed with a Malay population eight times as large with an ancylostome index of nil will in time yield a mixed population with an ancylostome index of 8·3 %.

Buddhism is said to have reached the Indian Archipelago about 223 B.C. and there are Javan traditions that about 300 B.C. thousands of families from N.W. India and from the Kling coast were established in Java.

Java and possibly other islands in Indonesia were subjected to Hindu domination for 14 centuries or up to the 15th century A.D. The temples date from about 600 A.D. This was followed by a Mohammedan invasion. Portions of Indonesia undoubtedly became seeded with *A. duodenale* at this time.

It seems probable that the present ancylostome formula of the mid-Javanese resulted from this Hindu invasion, for the high ancylostome index is found in those districts in Java where the Hindu culture, as evidenced by the presence of temples or their ruins, was most intense, that is to say in mid and East Java.

[1] Oldham (1905), *The Serpent and the Sun*, London.

There are no chandis in West Java and but few ancylostomes there. In the Preanger they (*A. duodenale*) are absent.

Beneath the cult of Mohammedanism in Indonesia there exists the remnants of Buddhism and Brahmanism. I have seen Javanese women who were nominally moslems actually worshipping in the ruins of a Brahman temple—a Hindu God. Underneath Brahmanism there yet lurks a pretty lively animistic cult, for the "hantu" or ghost possesses considerable influence in Malay households. Malay fishermen, at any rate in mid-Java, still attempt to propitiate by offerings of food the spirit which they believe presides over the destinies of fish and of fishermen, and thus modify the proverbial fishermen's luck.

Mohammedanism, Buddhism and Hinduism as well as Christianity have come to Indonesia from without.

It is possible that these cults in turn have been superimposed upon a pre-existing animistic cult or cults also due to outside agencies.

Perry[1] has called attention to the occurrence of stone monuments, dolmens, dissoliths, alignments and menhirs in Indonesia, notably in the Timor region, which bear certain resemblances to megalithic structures found in Burmah and Assam. He infers that the use of stone was not indigenous but was introduced from without to various parts of Indonesia. The new comers also introduced metal working, terraced irrigation and rice culture. These stone working migrants may have come from Burmah or Assam[2].

Whoever they were or at whatever period they made their appearance, if they contributed to the implantation of the ancylostome formula of the Timorese etc., it will be evident that they came from north of about 20° N. latitude.

This belief in the source of *A. duodenale* is based on information derived from worm findings among North Indians, Chinese and Japanese.

With regard to North Indians the information comes from two sources, North Indians examined in (*a*) the Malay States and (*b*) Fiji.

North Indians in the Federated Malay States.

These are represented by Sikh and Mohammedan Police from the Punjab. Some of these men had lived in the Federated Malay States ten or more years and their native or natural formula had possibly undergone some changes due to infection derived from Tamil, Malay and Chinese sources; however if we take only those men who had lived in the Federated Malay States ten years and under, there are 7 cases with a total of 41 hookworms, 21 of which were *A. duodenale* or an ancylostome index of 51·2 %. A second group from among hospital patients was made up of Sikhs and Bengalis, 8 persons, with a total of 222 hookworms of which 71 were *A. duodenale* or an ancylostome index of 32 %.

[1] Perry (1918), *The Megalithic Culture of Indonesia*, Manchester.

[2] There is however a trilithon at Haamonga, Tonga, which, according to tradition, was built by Polynesians (Samoans).

North Indians in Fiji.

Additional data and probably of greater value were obtained in Fiji from indentured and free coolies that had come directly from Calcutta. That is to say, they had embarked at Calcutta having been recruited from various places, for the most part north of 20° N. latitude—Central United and North West Provinces and speaking Hindustani—not Tamil or Telegu.

The information is of great value for there are no Chinese or other ancylostome bearing people on the island to complicate the species formula.

Thirty-four North Indians that had been brought out under indenture and had worked in the plantations five years and under were found to harbour 2480 hookworms, of which 684 were *A. duodenale* and the remainder *N. americanus*, the gross ancylostome index being 27·5 %.

The individual percentages vary from nil to 93 as is seen in the following table.

North Indians, Fiji. Years resident in Fiji.

1 year		2 years		3 years		4 years		5 years	
A. duod.	*Necat.*	*A. duod.*	*Necat.*	*A. duod.*	*Necat.*	*A. duod.*	*Necat.*	*A. duod.*	*Necat.*
33	11	51	5	31	17	9	17	8	27
21	197	3	38	28	98	19	83	47	74
30	20	56	36			4	29	53	347
1	6	24	247			29	64		
		31	24			8	16		
		5	6			0	17		
		17	25			1	1		
		5	2			39	3		
		15	3			3	20		
		23	8						
		43	101						
		16	7						
		20	83						
		5	90						
		1	58						
		5	16						

The free Indians or those who elected to remain in Fiji after their indenture had expired, were found after 7 to 14 years of residence to have lost a good many of their *A. duodenale* but to have become severely infected with *Necator* —the hookworm of the Fijians and of the country.

Among 35 *Free* North Indians the ancylostome index was found to be only 4·2 %—a striking illustration of the tendency of the index of the immigrants to approach that of the autochthones.

Other Asiatics from north of 20° N. Latitude.

Chinese.

The Chinese fall into two groups (*a*) those born in China who came to the Federated Malay States or Java as adults and (*b*) those born in Indonesia.

Chinese immigrants to Indonesia come from the Southern Provinces and

are known as Khehs, Cantonese, Hylams (Hainan) and Hockians. The new comers or "Sinkehs" of course bring with them typical worm formulas of their native country.

"Lowkehs" or men who have returned to Indonesia after a previous visit possess formulas altered possibly by previous residence.

It is not always possible to learn with accuracy a man's previous residence, for the Oriental is very guarded in replying to questions and may have reasons for wishing to appear as a new comer, this being particularly the case in Chinese who had been banished for crime.

At St John's Island, Singapore, we treated 46 "Sinkehs" and obtained 1241 hookworms of which 420 were *A. duodenale* and 821 were *N. americanus*, thus the ancylostome index was 33·8. In this group there were ten cases of pure *Necator* infection yielding altogether 148 worms. 36·9 % of the men had indices falling within the group index of 33·8.

Among the patients treated at the District Hospital, Kuala Lumpur, there were 79 Chinese who yielded 5191 hookworms, of these 1994 were *A. duodenale* and 3197 *N. americanus*, the ancylostome index being 38·4.

In this group there were 12 cases of pure *Necator* infection and 37 other cases whose indices were below the average for the whole group. The men had lived in the Federated Malay States for periods up to 20 years and possibly to some slight extent represent infection derived from other races. On the other hand the index is very close to that of Sinkehs and the index 38·4 or 33·8 in all likelihood represents a border line or frontier index, where the species overlap.

In five fatal cases of hookworm infection the ancylostome index was 86·1 %, there having been found 3779 *A. duodenale* and 698 *N. americanus*.

Chinese born in Indonesia.

Some data were obtained on the index of Chinese born in Indonesia, few cases it is true but very interesting as showing how children of the foreigners take up the worm index of the natives of the country.

Two Straits born Chinese were examined in Kuala Lumpur. One was of the first generation, the other of the second generation born in the Malay Peninsula. 72 worms were obtained from these young men, all *Necator*, the ancylostome index being nil.

Among the Chinese treated in the Batavia jail there were two born in Java. The man who was born in West Java had 123 hookworms, one of which was *A. duodenale*, a percentage of 0·8, which is a West Java index. The other who was born in mid-Java had 57 hookworms of which 11 were *A. duodenale*, giving a percentage of 19·3 which is a mid-Java index. Rather a striking illustration of the effect of regional soil in determining the species formula.

The physical resemblances between Malays and Chinese are very strong indeed. Wallace observed this in adults and even after having become

thoroughly familiar with the two races, I was at times unable to tell which of two sunburnt boys was the Malay and which the Chinese.

Yet close as the physical resemblances such as physiognomy, physique and cranial indices are, the helminthological testimony indicates that the Malays as a whole are no recent migrant stock from Southern China.

The Malays are not Chinese who have moved southward towards the equator and mixed with a dark skinned race, for the worm formula of the Malays is distinct from that of the Chinese. If the Chinese had migrated into Indonesia in hordes the ancylostome index of the Malays would approach that of the Chinese but this it does not do.

Some Malays may have moved northward and added their complement of *Necator* to an ancylostome-bearing Chinese stock, for the Chinese of South China to-day carry large numbers of *Necator* with their ancylostomes.

The presence of *A. duodenale* in mid and East Java, Madura, Lombok and Timor is not due to the presence of the relatively few Chinese coolies, traders or shopkeepers there, for the native population greatly outnumbers the Chinese. As a result we see the Chinese that are born in Java taking on the native index.

On the other hand where large numbers of *A. duodenale* carriers are present, as among the North Indians in Fiji, they are perceptibly infecting the native Fijians, just as we may suppose the Hindus or Burmese may have infected the Javanese of mid-Java centuries ago.

A small group of Japanese women, four in number, who had lived in the Federated Malay States three years and under were found to harbour 61 hookworms of which 19 were *A. duodenale*, giving an ancylostome index of 31·1. The index of the Japanese therefore resembles that of the Chinese and North Indians and is in marked contrast with the primitive index of people south of 20° N. latitude, that is, the Tamils, Malabaris and Malays.

Thus we see that there is a solid zone lying to the north within which the people have high ancylostome indices. It is from people in this more northerly zone that *A. duodenale* was introduced into mid and East Java and neighbouring islands.

South Indians.

Tamils, Malabaris and other Davidian natives of Southern India entering the Port Swettenham Quarantine Station were found to possess a uniformly low ancylostome index.

A series of treatments were carried out by Hacker and Barber on South Indian coolies, Tamils and Malabaris at Port Swettenham Quarantine Station.

From three squads, 31 persons, 4363 hookworms were obtained, 89 of which were *A. duodenale* giving an ancylostome index of 2·0.

This low ancylostome index among South Indians was encountered with great uniformity and serves to differentiate the North from the South Indians.

Twenty-five Malabaris that had lived in the Federated Malay States but

a few months yielded 3491 hookworms of which 30 only were *A. duodenale* and the remainder *N. americanus*, an ancylostome index of 0·86.

A group of 35 Tamil coolies engaged in road repairing in Kuala Lumpur were found to be harbouring 2870 hookworms of which 59 were *A. duodenale*, the remainder *N. americanus*, the percentage of ancylostomes being 2·0.

Polynesia.

Fijians represent a mixture of two stocks, Melanesian and Polynesian.

The typical Melanesian is exemplified by the Papuan, while the Polynesian is represented by the Tongan or Samoan.

Fusion of the two stocks is going on to-day in Fiji. With the object of learning what the species formula of the autochthonous Fiji population was, the remote and rather inaccessible village of Nasoqo in the mountains at the head waters of the Rewa River was visited and a group of 15 persons treated.

Among 546 hookworms obtained not a single *A. duodenale* was encountered, the ancylostome index being nil (a few *A. ceylanicum* were found as in the mountain villages of Java but these are derived from dogs and have no bearing on the *A. duodenale* index).

The worm counts made on the town dwelling Fijians (village of Nausori) confirm the findings at Nasoqo, but, as we have seen, they show evidences of contaminative infection by *A. duodenale* from North Indian sources, that is, from plantation and factory coolies working and living in the same village.

Until further and more detailed survey work is done in Polynesia we may assume that the primitive ancylostome index in this region is nil.

This observation at Nasoqo is of the greatest value, for it was made on a pure uncontaminated population of two fused South Sea ethnic stocks. Chinese, Japanese, Portuguese and East Indian immigrations have been for several years altering the primitive index of South Sea Islanders in the towns and villages near plantations.

The absence of *A. duodenale* in Fiji among uncontaminated autochthones indicates that races carrying *A. duodenale* as the Egyptians, Chinese, Burmese, Japanese and North Indians have never colonized there, and it shows that the Fijians, wherever their stock originally came from, did not come from north of 20° N. latitude and have never been in contact with people from those latitudes.

This is a matter of considerable interest in view of the probably erroneous opinion held by some that the Polynesians originated in northern Africa or Asia and that during their migrations southward they sojourned in Fiji.

Additional surveys are urgently needed in Polynesia before we can speak confidently in this matter.

To one who has been intimately acquainted with Malays and Javanese and has seen something of the Papuans, Solomon Islanders, Fijians, Tongans, Samoans and Maoris there is beyond certain linguistic similarities nothing to

suggest Malayan immigration to Polynesia, and these similarities may otherwise be explained.

FURTHER OBSERVATIONS AND CONCLUSIONS.

The hookworms harboured by a people depend on geographical, racial and climatic conditions and circumstances.

A people can only harbour the worm species which have been existing as embryos in the soil of their immediate environment.

The hookworms harboured by a person may disclose the influences to which he has been subjected in another environment.

The relative number and species of hookworms will sometimes furnish indications as to the ethnic origin of a people about whose history there is no record.

There has been a migration of rather large numbers of Asiatic people into parts of Indonesia.

These people came from north of 20° N. latitude, probably India or Burmah, and colonized in fairly large numbers in mid and East Java, Bali, Timor, Lombok and Madura as is evidenced by the hookworm species formula of the people now resident there. Other parts of Indonesia may have been visited as no doubt they were, but not by people in sufficiently large numbers to affect appreciably the normal formula of Indonesian people.

This Asiatic emigration did not extend to Polynesia, Fiji and Tonga for there are no helminthological evidences of it.

Whatever migration to the South Seas occurred, if any, it must have taken place by people from south of 20° N. latitude, that is, from Madras, or Malay Peninsula, Sumatra or other parts of Indonesia or previous to the Asiatic colonization of Java and Bali. That is to say by a people with an ancylostome index amounting to nil.

The presence of pure cultures or of relatively pure cultures of *Necator* in natives of Asia or Africa indicates that their hosts belong in the south rather than to the north, for the primitive distribution of *Agchylostoma duodenale* seems to have been limited to regions north of 20° N. latitude, while *N. americanus* was distributed south of this line.

A. duodenale may have been conveyed to or from the Orient along the old trade routes. But there are no evidences that *Necator* was introduced into Southern Europe from the east or into Egypt from South Africa for *Necator* is not found in Southern Europe or in Egypt. At any rate this species does not seem to be distributed to the latter places.

Careful surveys are necessary here as elsewhere, for it must be remembered that *N. americanus* was for years overlooked in India by British, Dutch and French doctors, although the species exists there in enormous numbers. Practically every East Indian over 14 years of age living north of Calcutta being infected with both species.

If certain tribes in America are found to be infected with *A. duodenale* as

well as *Necator* this will suggest their having come to this continent by way of the sea from those countries in Asia where *A. duodenale* and *Necator* are found to be infecting the natives, *i.e.* Japan and China.

A careful hookworm survey of existing Indian tribes may disclose the presence of more than one primitive stock. In other words: (*a*) a stock free from hookworms derived from Asiatic trans-Behring ancestors, (*b*) a stock harbouring both *A. duodenale* and *Necator* derived from Asiatic trans-Pacific ancestors, and (*c*) a stock with a pure *Necator* infection derived from Polynesian or Indonesian trans-Pacific ancestors.

If the Indian races or some of them living in regions unvisited by strangers are found to be free from hookworms this would furnish some grounds for supposing that the races in question had been derived from ancestors who had crossed from Asia by way of Behring Straits.

Surveys of all ethnic groups of people are urgently required before there occurs that mixing of stocks which will efface the individualities of species formulas.

Surveys are particularly desired in America among various North, South and Central American tribes, in Asia (subtropical), the Philippines, in Melanesia, Micronesia, Polynesia, Australia and in Madagascar and Easter Island.

THE ANOPHELINE WATERS OF SOUTHERN FLANDERS.

BEING A REPORT ON THE AREA OCCUPIED BY THE BRITISH SECOND ARMY IN FRANCE.

By A. D. PEACOCK, M.Sc., Captain R.A.M.C. (T.F.).

(With 1 Map and 1 Text-figure.)

Under instructions from Colonel W. W. O. Beveridge, C.B., A.D.M.S. (Sanitation), G.H.Q. France, a survey of the British Second Army Area in Southern Flanders was made in order to ascertain the condition of that region in regard to Anopheline mosquitoes. Permission to publish an account of the work has kindly been accorded by Lieutenant-General Godwin, Director-General of Medical Services.

A certain amount of similar work had already been performed by the writer in 1915 under instructions from Lt.-Col. J. Rutherford, A.D.M.S., 50th Division and also, in 1916, under instructions from Lt.-Col. H. Barrow, D.A.D.M.S. (Sanitation), Second Army, near the southern borders of the Second Army Area, and the results went to suggest that Anophelines would be found widely distributed and that, in certain areas at least, about one-fifth of the number of waters examined would harbour Anopheline larvae.

The first possibility was supported by the investigations in England of Nuttall, Cobbett and Strangeways-Pigg[1] and the later surveys of Grove, Parsons and Macdonald[2], in which it was ascertained that Anophelines could be found in all parts of England and Wales. The second possibility remained to be proved by further enquiry.

Regarding the species of Anophelines likely to be found, the late Prof. R. Blanchard, of the École de Médecine, in July 1918, informed the writer that he had records showing that Anophelines were generally distributed in the areas occupied by the French Armies, that is, in the country south-west of that in English occupation, the most common species being, as in England, *A. maculipennis*, while *A. bifurcatus* was less common and *A. plumbeus* (*nigripes*) had been but seldom found. Careful search for the last-mentioned however still remained to be performed.

[1] Studies in relation to Malaria, *Journal of Hygiene*, vol. I, 1901.

[2] Reports and Papers on Malaria contracted in England in 1917. *Reports to the Local Government Board on Public Health and Medical Subjects* (New Series, No. 119).

The data of this report have been derived from three sources:

(1) From surveys made by the writer during the summers of 1915 and 1916.

(2) From a survey made by the writer during September, 1918.

(3) From various collectors, the bulk of whose specimens had been collected during September, 1918, these specimens being identified by the writer.

SCOPE AND SCHEME OF WORK.

The main enquiry was commenced on August 30, 1918, and continued during the month of September, other duties preventing earlier and later investigations.

In view of the brief period of time available and the lateness of the season it was decided that the enquiry should be concerned with ascertaining, firstly and most importantly, how widely spread were Anophelines in areas most frequented by troops; and, secondly, if opportunity permitted, how high was the degree of infestation of any area or areas. In other words it was proposed to make a general survey and then, if possible, at least one detailed local survey.

As promising the speediest and most profitable return of information the plan followed was that of searching for the Anopheline breeding waters. The search for the haunts of the adults, involving laborious work among the dark places of rooms, cowsheds, stables and latrines, was regarded as too time-consuming and was not pursued. Again, except in a few instances, experiments in rearing larvae and pupae obtained from Anopheline and suspected waters, in order to determine the genus of the mosquitoes and the species of the Anophelines, were impracticable as also was the identification of the species of the Anopheline larvae captured.

The measure of success attained has depended a great deal upon the generous and ready help rendered by various sanitary officers and their non-commissioned officers and men. Intelligent work in searching for Anopheline waters was performed by these non-commissioned officers and men, who, from their civilian callings, were well fitted to assist in the investigation.

The co-operation of officers of the medical service was also invited, an illustrated circular and a pro-forma being distributed, the circular indicating the objects of the survey and detailing the methods of collection and despatch of specimens and information, while the pro-forma was designed to facilitate the forwarding of such specimens and information. These were distributed from the Office of the Director of Medical Services, Second Army, to all Deputy and Assistant Directors of Medical Services, Officers Commanding Stationary Hospitals, Casualty Clearing Stations, Mobile Laboratories and Sanitary Sections. In certain cases the A.D's.M.S. repeated the circular to Officers Commanding Field Ambulances and to Regimental Medical Officers. All the assistance rendered is acknowledged later.

TECHNIQUE AND METHODS.

The apparatus employed for dipping was the top of an infantry mess-tin, the inside of which was painted white to facilitate detection of the larvae. The handle was lashed to a stick about 3 feet long in such a way that the tin could be manœuvred into three positions (1) in the same straight line as the stick, (2) at an angle of 45° or (3) at right angles. With the co-operation of Lance-Corporal Hicks, 71st Sanitary Section, a more perfected little device was made and is here illustrated.

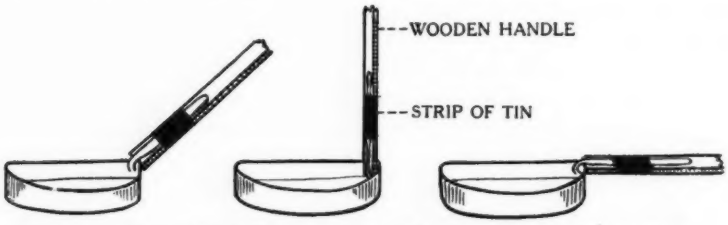


Fig. 1. Diagrams illustrating the device used in collecting larvae from water.

The strip of tin was tacked around the flat wooden handle so that a slot was formed for the insertion of the mess-tin handle. By altering the position of the mess-tin handle in the slot the device could be used rigid in the three different positions indicated.

The position of the dipper could be altered at convenience according to the character of the vegetation and banks of the water under examination, the third position being useful when skimming and to obtain specimens well away from the margin, and the second when the banks of the breeding water were high. Anopheline larvae were obtained by merely lowering the dipper into a pool or by scooping up the water but many methods had to be employed. It happened not infrequently that, while repeated scooping yielded no result, long skimmings of the surface among the vegetation were successful. In certain cases, when other methods failed, skimming the fringes of algae proved successful as did dippings taken at greater depths than the superficial two inches or thereabouts. No note in the negative was made in regard to a pool which looked at all promising for Anophelines till about 20 dippings proved fruitless.

Observations were recorded in a notebook on the spot.

THE ANOPHELINE CONDITIONS IN VARIOUS DISTRICTS.

The area bounded by imaginary lines joining the most outlying places visited, viz. Millam, Wylder, Woesten, Ypres, Kemmel, Armentières, Arques and Moulle, is approximately 350 square miles, but the area examined with varying thoroughness by all workers amounted to about 120 square miles only. Most of the districts of the complete area, however, have been touched and those described may be regarded as representative. Areas densely popu-

lated by soldiers and likely to remain so, naturally received the most attention. The conditions existing in 8 main districts and 12 isolated districts of the army area are described and certain observations from two other parts of the British military zone are also recorded. The 8 main districts have been named as follows: Advanced, Poperinghe, Hazebrouck, Southern, Rubrouck, Central, Waterlands and Armentières. In addition, observations were made in the vicinity of the following places: Houtkerque; Herzeele, Wormhoudt, Esquelbec and Zeggers Cappel; Arneke and Ledringhem; Steenvoorde, St Sylvestre Cappel, Cassel, Winnezeele and Abeele; La Motte; Ebblinghem; Wallon Cappel; Steenwerck; La Crêche; Le Romarin; Arques, Blendecques, Longpont and Mal Assise; Nielles lez Blequins; Clerques. The two districts outside the army area were Serqueux and Abbeville.

The general features of each district may now be described.

Advanced District. For military reasons this district could only be surveyed generally and certain special spots were selected as suitable places for search. The district is rectangular, 8 by $2\frac{1}{2}$ miles, with an area of 20 square miles and occupied the eastern side of the army zone. It had suffered severely from shell fire and the sites examined were much pitted with shell-holes. The number of sites examined was at least 220 but only 12 were found infested with Anophelines. In 8 cases larvae were found and in 3 the adult fly was taken near human habitations. Of the 12th there are no details. Of these 8 breeding waters, 5 were shell-holes, 2 were pools and 1 a stream. Of the habitations, 2 were medical aid-posts and 1 a billet. In 2 cases only were the larvae numerous. One observation from Ypres is important from the point of view of the number of Anophelines found. Out of 31 mosquitoes caught indiscriminately in an aid-post, 23 were *Anopheles maculipennis* ♀♀. At 2 centres, Dickebusch and Reninghelst, notwithstanding careful searching in many likely waters, negative results were obtained. The small number of infected waters is noteworthy and is difficult to explain. The character of the region in more quiet times did not appear different from the other regions which show a much higher proportion of Anopheline waters and the manner of search was the same as usually employed, so it is conceivable that the sparsity of infested waters may be attributed either to the lateness of the season or to the effect of poison gas used in fighting over this region or to both factors.

Poperinghe District. This irregular district has an area of about 40 square miles. It is mostly level farm land and is distinguished from most of the other districts described by the number of small woods it possesses. The method of search employed was to make a detailed survey of the land in the vicinity of the roads radiating for about 3–5 miles from Poperinghe and traversing the country to the villages Woesten, Elverdinghe, Vlamertinghe, Abeele, Watou and Proven, as well as of two other small regions (totalling 7 square miles), one in the neighbourhood of Hamhoek and La Lovie and the other

near Abeele and Hamhoek. Altogether about 12 square miles were inspected. Approximately 200 waters were examined, most of them farm pools, though streams, canals and shell-holes have also come under survey, and, in number and character, it is considered that this sample is representative of the district. Twenty-nine Anopheline waters were found, in 20 cases harbouring few larvae and in 8 harbouring many. One record is incomplete. That is, 14·5 per cent. of the waters examined contained Anophelines or about 1 pool in every 7, an average, also, of about 2·4 per square mile.

Hazebrouck District. This district is small, approximately 3–4 square miles, and is composed of open farm land. It contains the town of Hazebrouck and the village of Hondeghem. It was searched almost exhaustively and the results of the enquiry may be regarded as giving a correct idea of its condition in regard to Anopheline distribution. The number of waters was 114, practically all pools, of which 16 contained Anophelines, 9 with few, 4 with many and 3 with a number undetermined. The proportion of infested waters therefore was 14 %, or approximately 1 pool in every 7, an average of about 5 per square mile.

The results of the more general survey of the region north of the Hazebrouck district showed 7 infested pools out of the 53 investigated, that is, 13·2 % or about 1 in every 7 to 8 pools examined.

Southern District. This district, which is similar in character to the Hazebrouck district, was worked in detail for pools in the summer of 1916. It is irregular, about 20 square miles in area, the chief villages being Borre, Caestre, Pradelles, Strazeele, Fletre, Merris, Meteren and Neuve Eglise, with Bailleul as the important town. The only exact records preserved relative to this district are those concerning the location of the Anopheline centres and consequently the proportion of infested waters cannot be given. A general note exists which states that approximately 20 % were Anopheline but in view of the recent findings for the Hazebrouck district the statement cannot be accepted as final. As, however, the number of infested waters discovered was 64 it can be stated that there were 3 Anopheline waters per square mile.

Rubrouck District. This district, about 3 square miles in area, consists of open level farm country and the villages around which the survey extended were Rubrouck and Broxeele. The survey was a fairly detailed one but, being made by assistants, it is probable that certain infested waters were overlooked owing to the lack of training of these workers. Out of approximately 183 waters examined, 10 were found to be Anopheline, that is, 5·5 %, or 1 pool in 18, an average of 3 per square mile. The number of larvae was not noted by the observers.

Central District. This district of about 5 square miles includes the high-lying villages of Godewaersvelde, Boeschepe and Berthen and the land sloping away from them. The altitude rises abruptly to 200 feet above the sea level.

The waters examined lay in the vicinity of the roads intersecting the district and numbered 12, and were mostly pools. The comparatively small number is due to the fact that the waters appeared to be less numerous than in the surrounding lower-lying country. No Anopheline waters were discovered but in view of the small number of sites examined it cannot be asserted that no Anophelines existed.

Waterlands District. The waterlands of this part of Flanders are widespread and low-lying and are characterised by the presence of many canals which intersect them and the network of ditches of varying widths and depths. In the Second Army area the waterland region is irregular and not of great extent, being about 15–20 square miles. It penetrates the north-west boundaries of the army zone and is almost detached from the main waterlands to the north, the junction between them being narrow and running between high land on either side. The regions surveyed were part of the south-west fringe of the main waterlands, from Millam and Watten, about 1½ miles and the area bounded by imaginary lines joining Watten, Moulle, St Omer and St Momelin. The latter region is about 10 square miles in extent and is bounded on the east by the canal between Watten and St Omer, which receives all the drainage from the western network of streams and ditches. Particular attention was directed to pools in the vicinity of Moulle on the west, pools and ditches near Bleue Maison and Watten in the north, pools near St Momelin on the east and the main canal and a ditch running roughly north and south between Watten and St Omer. To the north, waters round the villages of Wylder and Rexpoede were investigated by Lance-Corporal Newman, R.A.M.C.

Near the village of Millam 4 Anopheline pools were discovered, 2 containing numerous larvae and 2 with few. The long ditch running by the side of the road from Millam to Watten was typical of the district. In width it varied from 4 to 8 feet and in depth to about 4. It received the drainage from smaller ditches on the eastern slopes. It was very rich in flora and the greater proportion of it was covered with water vegetation, open patches of water being exceptional. The predominant water weeds were marestail (*Hippuris*), starwort (*Callitriche*), duckweed (*Lemna*) and fringed water-lily (*Limnanthemum*) while water-cress (*Nasturtium*) and algae (*Spirogyra* mostly) were also present in places but, compared with the other plants, were small in quantity. Marginal rushes were also found but the banks were mostly grassy. The larger fauna consisted of eels (*Anguilla*), sticklebacks (*Gasterosteus*), fresh-water shrimps (*Gammarus*) and water hog-lice (*Asellus*). Examinations were made in at least 7 places along this ditch, many dippings being made at each examination but Anophelines were found in only two places and in small numbers. The first capture of 3 small larvae was made by repeatedly skimming the water above the algae and fringed water-lily, the second capture, 5 small larvae, by the same method above algae.

In the large district the following results were obtained. At Moulle three extensive sheets of water were examined. One, a large lake near the chateau, had a great deal of marginal duckweed and algae while the central water was more open but supported large floating mats of algae. The Anopheline larvae were of all sizes, extremely numerous and could readily be seen dotting the surface of the water. *This is one of the two waters which have been discovered to be highly infested and by reason of this and their large extent constitute real menaces.* Another small lake near by and of similar character, in spite of repeated search, yielded very few larvae, while a third gave a negative result. At Bleue Maison a few Anopheline larvae were found in a ditch overgrown with vegetation consisting mostly of fringed water-lily and tall sedges. At Watten two long ditches, each about 300 yards in length, and characteristic of the district, were examined intensively. They were mostly covered with duckweed, fringed with high rushes and had occasional open patches of water. No Anophelines were found. Another ditch running by the western side of the Watten—St Omer road, was also examined in detail. It was choked with high rushes and grasses and the surface was covered in many places with fringed water-lily and duckweed. The result was negative. The main canal was fringed in places with duckweed and grasses and stranded stalks of various plants but the results of many examinations were also negative. On the outskirts of St Momelin a small pool was discovered slightly infested. At Moulle, where the highly infested lake was situated, there was a dysentery camp for Chinese and a large Casualty Clearing Station—a dangerous association.

Twelve waters which included pools and ditches in the Wylder—Rexpoede district gave a negative result.

Armentières District. This district is of interest as showing, in contrast with most of the areas surveyed, the Anopheline conditions existing near a large town. In extent it is about 3 square miles and lies between Armentières and its outlying suburb Nieppe. About two-thirds is open, low-lying farming country. The examination was made in the summers of 1915 and 1916 and in the town showed negative results with regard to the infestation of receptacles such as water butts, ornamental pools and reservoirs. The canal also was negative. On the northern outskirts near the canal was a patch of low-lying, grassy, water-logged land which yielded numerous larvae. From the south-eastern suburb, Chapelle d'Armentières, one specimen of *A. maculipennis*, female, was brought to the writer. A mile to the east of the town a small Anopheline pool was discovered but no record of its degree of infestation has been retained.

Isolated Districts. The results obtained in the isolated districts examined may be given conveniently in tabular form.

District	Notes on Examination
Houtkerque; 1½ square miles.	About 18 waters examined; 1 Anopheline pool found; number of larvae not stated but probably few.
Herzeele; 1½ miles of road.	About 6 waters examined; result negative.
Wormhoudt, Esquelbec, Zeggers Cappel Road; about 4 miles.	About 15 waters examined; 1 Anopheline pool found.
Volkerinckhove; ½ square mile.	Nine waters examined; 2 Anopheline pools found; few larvae.
Arneke, Ledringhem; about ¾ square mile.	About 8 waters examined, 5 proving Anopheline; 3 being ditches, 1 a small marsh, 1 a pond; 4 contained few larvae. 1 (the marsh) had many.
Steenvoorde; roads radiating to St Sylvestre Cappel, Cassel, Winnezeele and Abeele; from 3–5 miles of each road taken.	About 30 waters examined, 3 proving Anopheline. A pool near Steenvoorde contained many larvae, a bomb crater in the same vicinity contained few, while from a pool in the town of Cassel a single larva was forwarded.
Ouderzeele; about 3 square miles.	About 20 waters examined with negative results.
La Motte.	Village surrounded by large woods; in and near the village 6 waters examined comprising 3 parts of the Canal de Nieppe, one lake, one pond and one ditch; 3 were Anopheline, one part of the canal and the lake yielding each 1 larva and another part of the canal 2 larvae; on the Hazebrouck Road 4 other waters were inspected, 3 ponds and the stream Bras de la Bourre; several were found at the margins of the stream, and in one pond they were numerous.
Ebblinghem.	Five waters examined showing one pond with a few larvae.
Wallon Cappel.	Eleven waters examined, yielding 3 ponds infested, 2 with few and 1 with numerous larvae.
Steenwerck.	No details.
La Crêche.	Anopheline pool; larvae numerous.
Le Romarin.	Anopheline pool; larvae few.
Arques, Blendecques, Longpont, Mal Assise.	About 8 waters examined yielding 4 infested; one was a ditch, the second a pool—both with few larvae, the third, a ditch, contained an extremely large number and in the fourth, a pool, they were numerous. Adult Anophelines (*maculipennis*) were found in Blendecques.
Nielles lez Blequins.	Few larvae found in a pool.
Clerques.	Three waters in vicinity examined; one Anopheline larva in one pool.

Notes on Anopheline districts in France outside the Second Army Area. Anopheline larvae were found among a sample of many hundreds of Culicine larvae sent by Capt. Wadsworth, R.A.M.C., from Serqueux. The pond from which they were obtained was in close proximity to a malarial segregation hospital. The specimens were collected on August 22nd, 1918. At Abbeville between August 22nd and 25th, 1918, were found 3 large Anopheline ponds and one water channel in the Faubourg Thuison, one of the ponds containing numerous larvae and the other two containing few, while the channel also yielded few. Larvae were also found in the marginal vegetation of a stream running through the Triage (goods station) and at Mautort, some 3 miles outside Abbeville, 3 large Anopheline pools were discovered, one with numerous larvae and 2 with few.

GENERAL NOTES ON THE ADULT AND LARVAL ANOPHELINES FOUND.

At various times during 1915, 1916 and 1918 about 40 adult Anophelines of this area have been examined by the writer and all proved to be *A. maculipennis*. Of this number 27 were captured wild and the remainder reared from larvae or pupae. Only two of these were males, both being hatched in captivity. In addition Father Legros, R.C., C.F., informs me that specimens which he collected alive at Moulle and which were identified for him at the British Museum proved to be of the same species. No records or specimens of *bifurcatus* or *plumbeus* (*nigripes*) have come to the writer's notice in this region.

A certain amount of interest is attached to the capture by Capt. Rankin, R.A.M.C., of 23 *maculipennis, all females*, out of a total catch of 31 mosquitoes obtained in an afternoon from the inner gas curtain of a dark, damp aid-post. No discrimination was exercised in taking the specimens. This is the only relatively large catch of adults which has come to the writer's notice in Flanders, all other catches yielding usually one, and not more than two, specimens.

The proportion of Anophelines to Culicines cannot be stated even approximately but judging from general observations on larvae and adults it must be very small.

As regards the larvae captured during September 1918, the only remark that may be made is that no seasonal preponderance of any one size of larvae could be detected.

NUMBER, NATURE AND CHARACTER OF ANOPHELINE WATERS DISCOVERED.

The total number of examinations made was at least 1233, all except 12 relating to waters, these 12 exceptions referring to adult specimens captured. The exact number of examinations is uncertain as certain collectors forwarded approximations only of the number of waters coming under their survey. Of the total number of examinations, about 558 were made by the writer—at least 210 in the summers of 1915 and 1916, and 348 during the month of September, 1918—and 675 by the various collectors. Out of these 1233 records, 178 show the location of Anopheline haunts. The proportion of Culicine waters cannot be estimated as collectors have not furnished full enough details, most contenting themselves with noting the Anopheline waters only. Of the 178 Anopheline haunts 133 were discovered by the writer, 67 in 1915 and 1916 and 66 in 1918, and 45 by collectors, 5 in 1915 and 1916 and 40 in 1918. Only 5 of the Anopheline records refer to adults. The nature of the 173 Anopheline waters is given in the following table.

Analysis of the types of 173 *Anopheline waters discovered.*

Pools, etc.	127 (73·4 %)	Pools, 121; lakes, 2; moats, 4.
Holes	16 (9·25 %)	Shell-holes, 8; pits, 8.
Streams, etc.	12 (6·9 %)	Streams, 9; canals, 3.
Ditches	8 (4·6 %)	Includes one small stream in which water was very low and stagnant.
Marsh, etc.	6 (3·5 %)	Marshes, 5; water-logged field, 1.
Receptacles	2 (1·2 %)	Tin*, 1; concrete basin, 1.
No details	2 (1·2 %)	

* On another occasion, numerous larvae were found in a petrol tin, cut to make an ablution basin, stranded in the mud at the side of an Anopheline pool.

The term "pools" refers principally to waters found in the farm-lands and for the most part lying in clayey soil. Many of these are natural but many undoubtedly are really waterholes of artificial origin having been dug in years past by farmers for use by cattle. These waterholes are usually circular, comparatively small, varying from about 20–60 feet in diameter, and are usually surrounded by pollard-willows. Their vegetation varies, some being clear of weeds, others with marginal weeds and algae more or less loosely distributed while others again have a dense mat of duckweed completely hiding the water. Moats with vegetation similar to that of pools are found round many of the farms and chateaux. The term "canal" is used in the strict sense of the word. In one case the map refers to certain water as a canal when the water really takes on the character of a narrow stream running fairly rapidly. This has been classified as a stream.

The character of the Anopheline waters in regard to possible pollution from various sources has been noted nine times; on four occasions the water being described as "dirty"; once as "tea-coloured," the reason for such a colour being unknown; once as "greenish with numerous larvae," the green possibly due to cow manure and not to confervoids; once as "brown, not a likely place"; once as "poor quality, unusual place"; once as "containing some pollution." In one case where the water was dirty the circumstances were exceptionally interesting. The pool in question was circular and about 60 feet in diameter, with many high sedges and a certain amount of duckweed at the margin. The water was black and turbid. Into one region ran the effluent of the inefficient soakage pit of a hospital bath-room, the effluent water being still soapy. Opposite this the pool drained into a narrow channel running through a culvert. Altogether a most unlikely spot for Anophelines! But near the entrance to the culvert both Anopheline and Culicine larvae were taken. The Anophelines did not show any unusual features but the Culicines presented a remarkable appearance as if they were covered with a white fungoid-like growth. This was probably due to the soap suds from the effluent. In another instance larvae were found in a small marginal patch of water surrounded by the marginal grass of a pool reddened by the rust of ration

tins which had been thrown into it. Ten waters, rendered disturbed or turbid through rain, also contained Anopheline larvae.

The floral and faunal associations of the Anopheline larvae.

(*a*) *Floral.* Out of 106 records the following analysis results:

Flora	Number of times during which Anopheline larvae were found associated
Grass	18 (17 %)
Grass predominating, with the addition of confervoids and the common waterweeds	17 (16 %)
Algae—mostly *Spirogyra*	18 (17 %)
Algae—with addition of broad-leaved pond-weed (*Potamogeton*), water-cress (*Nasturtium*), fringed water-lily (*Limnanthemum*), duck-weed (*Lemna*), flag (*Iris*)	11 (10·3 %)
Water-cress	6 (5·6 %)
Water-cress predominating, with addition of other vegetation	2
Sedges (*Carex*) and other vegetation	2
Confervoids	2
Broad-leaved pond-weed and duckweed	2
Rushes (Juncaceae) and algae. Rushes and marestail (*Hippuris*). Lily and algae. Fringed water-lily and sedges. Flag. Flag and duckweed. Weed unidentified	Each 1

On six occasions larvae were found in water with no visible foodstuffs. Fifteen records are incomplete. Waters in which the visible vegetation was grass or algae or predominately either of these gave positive results almost certainly. Association with water-cress was not infrequent. In ponds covered entirely with a dense mat of duckweed Anophelines have never been found but at the margins of certain pools of this character, in open patches of water among tall fringing vegetation, the larvae have been taken. The low degree of infestation of the ditches of the waterlands is interesting.

(*b*) *Faunal.* The results of 167 records show the following:

Fauna	Number of times during which Anopheline larvae were found associated
Culicine larvae alone	40 (24 % nearly)
Water hog-louse (*Asellus*) alone	11 (6·5 %)
Fresh-water shrimp (*Gammarus*) alone	2
Culicines and water hog-lice	5
Culicines, water hog-lice and fresh-water shrimps	1
Water hog-lice and fresh-water shrimps	1

The number of times during which Anopheline larvae were found alone was 109 (65 % approximately). Fresh-water fish of many kinds have also been found along with Anophelines. Water-boatmen (*Notonecta*) have been observed, in an aquarium kept at a Casualty Clearing Station, to prey upon and suck Anopheline larvae.

The conclusions, therefore, are that waters with a vegetation consisting of grass or algae or with vegetation in which grass or any alga is predominant are almost entirely Anopheline and that all waters should be regarded as suspected Anopheline habitats.

The Degree of Infestation of Anopheline Waters. In regard to the number of larvae found in the waters it has been found necessary to establish a standard by which to estimate the degree of infestation of such waters.

While the number of dips taken at a water varied with the conditions discovered, the result of usually 20 dips per water, taken at various parts, was judged to indicate the degree of infestation, and, in practice, it was found that the catches yielded extremes, there being captured either few or many. The term "few" refers to *total* catches up to 10 or thereabouts and the term "numerous," interpreted rather broadly, to those in which the average yield *per dip* was 3 and over.

The number of records is 106, from which it is found that the number of waters with few larvae was 67 (63·2%), those with numerous larvae 22 (20·7%), while 17 (16·1 %) records are doubtful.

It was impracticable to ascertain the Anopheline population of any water but it may be recalled that in two instances, at Moulle and Arques, it would run into many thousands.

The Degree of Anopheline Infestation of the Second Army Area. In estimating the significance of these results regard must be taken of the comparatively few pools examined in certain regions, the inexperience of some of the collectors and the lateness of the season. These factors would tend to produce results which would indicate that the number of Anopheline waters and the degree of infestation of the districts were lower than those actually obtaining.

The weather conditions during the survey, on the whole, were good for the season of the year, there being a number of hot days. For about seven days the weather was wet, bleak and cold but it is unlikely that it influenced the results to any great extent.

In estimating, from the data discovered, the Anopheline conditions existing in the Second Army area three questions must be answered, viz.:

(1) What is the geographical distribution of Anopheline waters?
(2) What proportion of waters is infested with Anophelines?
(3) What is the degree of infestation of these waters?

In regard to (1) it can be stated that Anophelines are generally distributed throughout the Second Army area. Out of 20 neighbourhoods examined, only in 4, Herzeele, Ouderzeele, Steenvoorde (south and west) and Godewaersvelde, Berthen and Boeschepe (high land), were no Anophelines found, but it is quite probable that more careful search would yield positive results. It may also be added that the greater number of Anopheline waters were in close proximity to billets.

In answering the questions (2) and (3) it would be incorrect to total the

findings for all the districts and then strike averages because the different districts vary in their characters and have been surveyed with varying thoroughness and skill. It seems fairest, therefore, to take the results obtained in a district which, in its physical features, is representative of the greater part of the Second Army area and which has been carefully and thoroughly surveyed. Having regard then, to the season of the year when the investigation was made, the findings of the Hazebrouck district are selected as representative. The findings are:

Proportion of waters infested with Anophelines	14 % about 1 in 7
Number of Anopheline waters per square mile	5
Proportion of Anopheline waters with numerous larvae	25·0 %
„ „ „ few „	56·3 %
„ „ „ undetermined number of larvae	18·7 %

As a matter of interest the findings for the Poperinghe and Southern districts, which were surveyed in fair detail, and the whole Second Army area, as well as the findings for certain eastern counties of England are given in the following table. The figures relating to England have been obtained from the writer's analyses of the data of 64 waters given by Nuttall, Cobbett and Strangeways-Pigg[1]. Similar figures to these with regard to the

Table showing comparison between the degrees of infestations of various districts in Flanders and England.

Particulars	Hazebrouck District: Standard	Poperinghe	Southern	Whole Second Army area	Eastern counties* of England, July and September, 1900
Percentage of waters infested with Anophelines	14·0 %	14·5 %	20 % (?)	14·0 %	—
Number of Anopheline waters per square mile	5	2·4	3·2	1·4	—
Percentage of Anopheline waters with numerous larvae	25·0	27·5	?	20·7	56·25†
Percentage of Anopheline waters with few larvae	56·25	69·0	?	63·2	29·7
Percentage of Anopheline waters with doubtful number of larvae	18·75	3·5	?	16·1	14·0

* Counties of Lincolnshire, Norfolk, Suffolk, Cambridgeshire, Huntingdonshire, Bedfordshire, Hertfordshire, Essex and Kent.

† 48·4 % numerous, 7·85 % fairly numerous.

later finds of Grove, Parsons and Macdonald[2] in England cannot be made from their reports. This is unfortunate as these investigators have surveyed districts where cases of malaria have recently occurred among troops and civilians who have never been out of the British Isles.

It will be noticed that the proportion of English Anopheline waters which contained numerous larvae was much greater than that of the Flemish waters.

How the degree of infestation of the Flanders region would compare with other areas in European countries in the temperate zone cannot be given, as

[1] *Loc. cit.* [2] *Loc. cit.*

the subject, to the writer's knowledge, has not received sufficient attention. The evidence given above, however, would seem to indicate that, from an absolute standard, the degree of infestation for the Flanders region is low.

Comparisons can only be made then from existing standards which are all concerned with conditions existing in sub-tropical and tropical countries. To illustrate, a few examples may be cited from countries in the various theatres of war. In Italy, in 1900, Grassi caught 200 adult Anopheles during a two hours' coach ride across the plains of Capaccio[1]; in Macedonia "the quantity of *Anopheles* reaches absolutely extraordinary proportions in some regions, it being possible to catch hundreds of dangerous mosquitoes in a few hours[2]"; in Palestine, I am informed by Capt. Adams, R.A.M.C., he found 30 % of the wells etc. in Jaffa to be Anopheline. From the number of larvae found in Flanders and, bearing in mind that only a proportion of larvae reach maturity, it may therefore be safely asserted that the degree of Anopheline infestation of Flanders is very low compared with that of these sub-tropical malarious countries.

THE PROBABILITIES OF THE SPREAD OF MALARIA AMONG TROOPS IN SOUTHERN FLANDERS.

In estimating the probabilities of an outbreak of malaria among the troops in the area surveyed two other considerations had to be taken into account:

(1) How many troops and civilians were malarial subjects.

(2) What had been the incidence of "primary" malaria among troops from non-malarial districts of the British Isles.

Owing to the insufficiency of the epidemiological evidence it is impossible to discuss these in anything but a general way. Undoubtedly many divisions of troops which occupied the area contained a high proportion of malarial subjects as, for instance, the Indian Division which occupied the area as early as 1914–1915, and a succession of colonial troops, old and new army divisions which had served in the Eastern Fronts, as well as Chinese and coloured labour corps. My only information as to the incidence of malaria among civilians is meagre and was received from Major McNee, D.S.O., R.A.M.C., who stated that he had been informed by a local general practitioner that an outbreak of malaria had occurred about 1905 at Steenwerck. However, from the military evidence alone it is certain that the district has never had such a large and varied population of human malarial hosts, even during the conditions which may have existed in the many campaigns conducted over this historic fighting ground.

At the time of writing an insignificant number of troops had contracted "primary" malaria.

[1] Cited by Nuttall, Cobbett and Strangeways-Pigg (1901).

[2] Armand-Delille, Abrami Paisseau and Lemaire. *Malaria in Macedonia*, Military Medical Manuals, 1918.

All factors considered, then, it would seem that there was little likelihood of an epidemic of malaria occurring in the British Army in Flanders. Still less likely is an outbreak to-day among the civilian population. Further, as will be shown presently, even in the event of an outbreak, the entomological conditions are easily amenable to control.

NOTES ON CERTAIN PREVENTIVE MEASURES.

The object of this section is merely to indicate certain conditions which were peculiar to the existing circumstances and which would have demanded special consideration in the event of the institution of prophylactic measures.

Military exigencies permitting, a great deal of most useful preventive work would have been easily practicable owing to the type of Anopheline waters existing in this zone. Most of these are pools of comparatively small size and thus amenable to treatment by the usual methods of dragging them free of weeds and oiling. If all such habitats were treated successfully the Anophelines of the area would be brought under control.

In the case of certain pools important considerations would arise when deciding what action should be taken when the Anopheline water was (1) the sole source of supply for military horses, (2) the sole source of supply for civilians or their farm stock.

The first difficulty could be overcome in certain cases by digging a separate small water-hole at the side of the pool, and then periodically treating the pool. In this way water could be obtained which would not offend the sense of smell of horses. In many cases a water-hole would be unnecessary as many transport units are provided with pumps and hose which permit the withdrawal of water from below the surface.

In the second instance arrangements would have to be made with civilians, through the usual authorities, that their water should be treated but that they could obtain necessary supplies from the same source as the military.

In conclusion, all sites of malarial segregation camps, permanent hospitals and depots, and the camps of coloured troops and Chinese labourers would have to be carefully chosen. In the event of such places being compulsorily near Anopheline waters it would be necessary to put rigorously into practice the usual preventive measures.

ACKNOWLEDGMENTS.

The writer desires to record, with grateful acknowledgments, the names of those officers, non-commissioned officers and men who so willingly assisted in the survey and, at the same time, to note the nature of the services rendered. Major Dale, D.A.D.M.S. (Sanitation) Second Army, was responsible in arranging that my movements were free and unhampered. He also collected and forwarded specimens. The following officers commanding sanitary sections of the R.A.M.C., as well as affording me pleasant hospitality, arranged means of transport and detailed assistants from their units: Captains Porter,

Bryce, Murray, Reed, Sands and Lieutenant Regan. Specimens and information were received from Captains Bain, Rankin, Johnstone, Armitage, R.A.M.C. and Lieutenants MacDonald and Saltmarsh, R.A.M.C. (T.F.) (London Sanitary Coy.). The assistant surveyors who performed so much intelligent work were Corporal Barnes, Lance-Corporals C. Roe, W. Roe and Gudger and Privates Hargreaves and Walden all of the sanitary service.

SUMMARY.

(1) The object of the investigation was to ascertain the condition of the Second Army area of Southern Flanders in regard to Anopheline mosquitoes.

(2) The data of this report have been derived from three sources (1) from the writer's surveys during the summers of 1915 and 1916; (2) from the writer's survey of September 1918; (3) from various collectors the bulk of whose specimens were collected during September 1918.

(3) Circumstances determined that the method of investigation should deal almost exclusively with breeding waters. Except on a very small scale no attempt could be made to rear larvae and pupae or capture adults.

(4) The distribution of a circular and pro-forma resulted in a certain amount of information being obtained from medical officers and officers commanding sanitary sections. Valuable assistance was also rendered by certain non-commissioned officers and men.

(5) The surveyed area of the Second Army zone bounded, roughly, by imaginary lines joining the places Millam, Woesten, Ypres, Kemmel, Armentières, Arques and Moulle was about 350 square miles; most of its districts were touched upon, their areas totaling about 120 square miles; eight main districts and 12 isolated districts, representative of the country, were surveyed with varying thoroughness and skill; the main districts were the Advanced Zone, Poperinghe, Hazebrouck, Southern, Rubrouck, Central, Waterlands and Armentières.

(6) Out of 40 adult Anophelines, caught wild or reared from larvae and pupae, all proved *maculipennis*.

(7) Twenty-three *A. maculipennis, females*, were caught in one afternoon in a dark, damp medical aid-post.

(8) No seasonal preponderance of any one size of larvae was observed during September 1918.

(9) Out of about 1233 records of sites inspected, 178 refer to Anopheline haunts, 5 referring to captures of adults.

(10) Of the 173 Anopheline waters discovered 127 (73·4 %) were pools or lakes, 16 (9·25 %) were holes (shell-holes or pits), 12 (6·9 %) were running waters (9 streams, 3 canals), 8 (4·6 %) were ditches, 6 (3·5 %) were marsh, 2 (1·2 %) were receptacles (1 a tin and 1 a concrete basin); 2 records give no details.

(11) From 106 records the number of waters with few Anopheline larvae (up to about 10) was 67 (63·2 %), with numerous larvae (3 and more per dip)

22 (20·7 %); 17 (16·1 %) records are doubtful. In 2 cases the number of larvae was many thousands.

(12) On 9 occasions Anopheline larvae were found in polluted water.

(13) Anopheline larvae were found almost certainly in all waters where the visible vegetation was grass or algae or predominantly one of these. Association with water-cress was not infrequent. Ponds entirely covered with a dense mat of duckweed never gave Anopheline larvae but, at times, such pools may have open patches among marginal vegetation and in these patches the larvae have been taken. They have also been found in water which showed no visible foodstuffs.

(14) Anopheline larvae were found alone in 65 % of cases, and co-existing with Culicine larvae in 24 %, with water hog-lice (*Asellus*) in 6·5 % and with fresh-water shrimps (*Gammarus*) in 1·2 % of cases; they may also co-exist with any two or all three of these, and with fresh-water fish of many kinds.

(15) Water-boatmen (*Notonecta*) have been observed in an aquarium to prey upon and suck the juices of Anopheline larvae.

(16) All waters are suspect.

(17) It is probable that further summer work would show the number of Anopheline waters and the degree of infestation of the districts to be higher than the results here cited.

(18) Anophelines have been found generally distributed all over the area and in close proximity to billets. In 4 districts out of 20 examined, none was found, but more careful search would probably reveal them.

(19) The results obtained in the Hazebrouck district are taken as representative of the approximate degree of Anopheline infestation to which the Second Army area attained. The findings are (1) 14 % (1 in 7) of waters examined were Anopheline; (2) there were 5 Anopheline waters per square mile; (3) 25 % of Anopheline waters contained numerous larvae and 56 % contained few; of the remainder there is insufficient record.

(20) Generally speaking, and as far as information of the conditions obtaining in other regions in the temperate zone permits comparison, the degree of Anopheline infestation of the whole area appears to be low; compared with sub-tropical regions formerly war zones—Italy, Macedonia, and Palestine —it is very low. Two districts, Moulle and Arques, showed waters highly infested, both being in the neighbourhood of hospitals. The ditches of the Waterlands district showed a low degree of infestation.

(21) The nature and character of the Anopheline waters render them amenable to treatment by dragging of weeds and oiling and, military exigencies permitting, sufficient preventive measures could be instituted to bring Anophelines under control.

(22) Notwithstanding that the area has been densely populated with a great variety of malarial troops and that a few cases of "primary" malaria have occurred, an epidemic of malaria among troops or civilians is unlikely.

(23) In instituting preventive work under war-conditions cognizance

should be taken of conditions in which Anopheline waters are the sole watering places for military and civilian needs; also, sites for hospitals and large permanent camps likely to house malarial subjects should be carefully chosen and kept free from Anophelines.

CONCLUSIONS.

(1) The commonest Anopheline mosquito in the area is *A. maculipennis.*

(2) The proportion of Anopheline waters in this area reached 14 %, *i.e.* 1 pool in every 7 is Anopheline.

(3) The number of Anopheline waters per square mile reached 5.

(4) The proportion of Anopheline waters with numerous larvae reached 25 %.

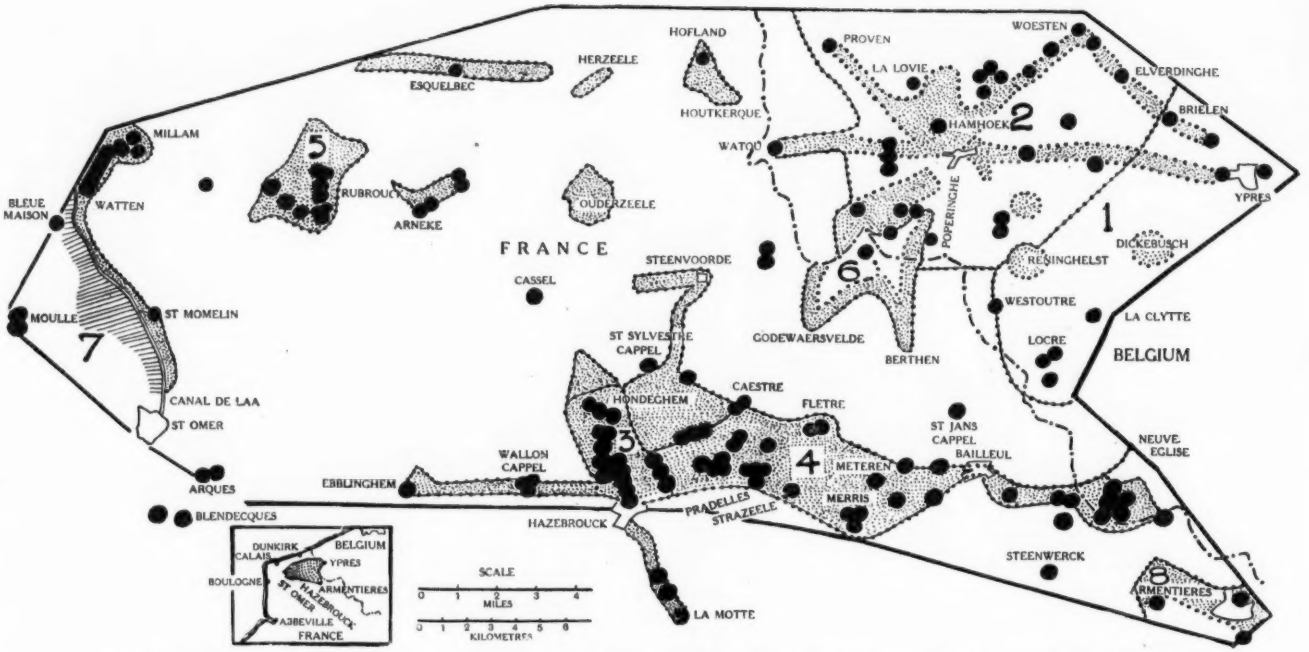
(5) The degree of Anopheline infestation appears to be low, absolutely, and in comparison with conditions in sub-tropical countries, very low.

(6) Two districts, Moulle and Arques, are exceptionally highly infested for this area.

(7) All waters, particularly those with vegetation consisting of grass or algae, are suspects.

(8) An epidemic of malaria is unlikely in this area.

(9) Military exigencies permitting, the problem of controlling Anophelines in the area ought not to be difficult.



MAP SHOWING THAT PART OF SOUTHERN FLANDERS WHICH WAS SURVEYED FOR ANOPHELINE WATERS.

The main districts are:—1 Advanced; 2 Poperinghe; 3 Hazebrouck; 4 Southern; 5 Rubrouck, 6 Central; 7 Waterlands; 8 Armentières. Their boundaries are indicated by either —•—•—•— and ————, or —•—•—•— only, according to their situation. The land traversed is indicated by stippling.

The large black spots mark the position of Anopheline infested areas, the infested water occupying a position indicated by the centre. Each water is assumed capable of infesting the surrounding district for a radius of ¼-mile, that distance being, approximately, the range of flight of an Anopheline. The dots therefore are drawn to indicate circular areas with a radius of ¼-mile.

—•—•— Boundary between France and Belgium. ═══ Land intersected by water ditches. Inset: Map to show situation of area surveyed.

ON THE CLASSIFICATION OF THE ASCARIDAE.

I.—THE SYSTEMATIC VALUE OF CERTAIN CHARACTERS OF THE ALIMENTARY CANAL.

By H. A. BAYLIS, M.A.

(With 1 Text-figure.)

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INTRODUCTION.

The great French helminthologist, Dujardin, appears to have been the first to suggest a grouping of the genus "*Ascaris*" according to the structure of the alimentary canal. As is, unhappily, only too well known to modern helminthologists, little attention was paid to internal structures by the earlier workers, whose numerous descriptions and classifications were based almost entirely upon external characters. It is now recognized that a natural system must be based on a survey of the whole structure of the animal, both external and internal, and a re-examination of many of the older species becomes extremely important.

While some families of Nematodes have received considerable attention in recent years, and materials for a natural grouping are gradually accumulating, the Ascarid family seems to have been comparatively neglected, perhaps because of the extremely large number of species, to which every year still more are being added, and which seems to make it an almost hopeless task to reduce them to a natural, orderly and convenient systematic arrangement. Hall (1916), in the course of some introductory remarks to his valuable revision of the Nematodes of Rodents, has mentioned that in the index catalogue of the Zoological Division of the United States Bureau of Animal Industry something like a thousand species are enumerated under the generic name "*Ascaris*." Stossich (1896), in his monograph of the Linnean genus, mentions 218 species. Of course, many of the so-called "species" are no doubt synonyms, misdeterminations, or otherwise inadmissible; but, even allowing for this, the "genus" is intolerably unwieldy, and it is clearly time that effective steps were taken to split it up into smaller groups, if only for the sake of convenience.

The process of splitting-up has been carried on in a desultory manner since Dujardin's day, but has not, up to the present, led to any highly satisfactory results. No uniform system has been adopted by the various workers

who have approached the subject, and the limits and contents of the families and subfamilies that have been created are very ill-defined. The present position, in general, is that the Linnean genus *Ascaris* has risen to the rank of a superfamily, Ascaroidea, with the families Ascaridae, Heterakidae and Oxyuridae. These families, again, have been variously subdivided into subfamilies, while there is a tendency, as always in the progress of systematic zoology, for the subfamilies themselves to be raised to the rank of families.

The System of Dujardin.

We may now return to the consideration of the system outlined by Dujardin (1845). Having separated off as "subgenera" the forms which now compose the families Heterakidae and Oxyuridae from the "true Ascarids," Dujardin places the latter in a "subgenus," *Ascaris*, which he further divides into four sections, taking the structure of the alimentary canal as a basis for the classification. His four sections are as follows (translating as closely as possible the original characterizations):

Section 1. "Ascarids with simple oesophagus with or without ventriculus, but without pyloric appendices."

In this section are placed the whole of the forms known from mammals, the great majority of those from birds, reptiles and fishes, and one from an insect.

Section 2. "True Ascarids in which the oesophagus is followed by a more or less distinct ventriculus and accompanied by a pyloric caecum or appendix springing from the intestine."

This section comprises the following forms:

	Hosts
A. gypina Duj.	Vultures.
A. depressa Rud.	*Falco*, etc.
A. spiralis (Zeder)	Owls.
A. ensicaudata (Zeder)	*Turdus* spp.
A. crenata (Zeder) (prob. = *ensicaudata*)	*Sturnus*.
A. heteroura Crepl.	*Charadrius*, etc.
A. semiteres (Zeder)	*Vanellus*, etc.
A. praelonga Duj.	*Colymbus*.
A. crassa Deslongchamps	*Anas*, etc.
A. constricta Rud.	*Trachinus*.
A. incurva Rud.	*Xiphias*.
A. ecaudata Duj.	*Conger*.

Section 3. "True Ascarids in which the oesophagus is prolonged by a pyloric caecum or appendix alongside of the intestine, and itself accompanied by another caecum springing from the intestine and forwardly directed."

Here are placed the following species:

	Hosts
A. spiculigera Rud.	Cormorant, Pelican.
A. pedum Deslongchamps	*Scomber*.
A. obtusocaudata (Zeder)	*Salmo*, etc.
A. adunca Rud.	*Clupea*.
A. clavata Rud.	*Gadus*, etc.

Section 4. "True Ascarids having a single pyloric caecum or appendix springing from the oesophagus, posteriorly, alongside of the intestine."

A single species,

	Host
A. acus Bloch.	The Pike (*Esox*).

This résumé of Dujardin's system has been given because it seems to have been generally either forgotten or ignored by more recent workers, some of whom have actually created new genera for forms having exactly the characters given by Dujardin for one or another of his Sections 2, 3 and 4, without mentioning the fact that Dujardin had already noticed them, and without comparing the new forms with those included in Dujardin's groups.

During recent years an attempt has been made by Railliet and Henry (1912) to group together all the Ascarids in which oesophageal or intestinal diverticula occur. They thus created the subfamily Heterocheilinae, which they have subsequently (1915) shown a desire to elevate to the rank of a family, Heterocheilidae. More recently still, Gedoelst (1916) has given a dichotomous table of forms referred by him to the Heterocheilinae (apparently not accepting the group as of family rank) to which he has added a new genus, *Dujardinia*, for the reception of *Ascaris helicina* Molin. The table is based on the following features, which are here given in the supposed order of importance:

(1) Presence or absence of intestinal and oesophageal caeca.
(2) Presence or absence of interlabia.
(3) Presence or absence of dentigerous ridges.

In the course of the following remarks it will be necessary to inquire whether this subfamily (or family) can be regarded as a natural group, and to see, if possible, to what extent the presence or absence of caeca connected with the alimentary canal provides a sound basis for classification.

Data derived from a re-examination of species.

With the idea of obtaining some more definite knowledge of the occurrence of these modifications of structure in the alimentary canal, and of the relationships, if any, between the forms in which they are found, a number of species of Ascarids available in the British Museum have been re-examined expressly from this point of view, note being also taken of the presence or absence of interlabia and dentigerous ridges—points usually assumed to be of systematic value. The list of species so examined at present is very limited, but the results already appear to the writer to indicate that the occurrence of such structures is more widespread among the Ascaridae than has hitherto been realised, and that it may have a very important bearing upon the ultimate systematic grouping of these forms.

The species[1] of which specimens have been re-examined at present are the following:

	Hosts of actual material
Ascaris aucta Rud.	*Blennius viviparus, Rhombus punctatus.*
„ *decipiens* Krabbe	*Otaria jubata.*
„ *depressa* (Zed.)	*Gyps fulvus, Accipiter nisus,* "eagle."
„ *colura* Baylis	*Lophoaëtus occipitalis.*
„ *ensicaudata* (Zed.)	*Turdus merula, T. musicus, Sturnus vulgaris.*
„ *halichoris* Owen	*Dugong,* sp.
„ *holoptera* Rud.	*Testudo graeca, T. mauretanica, T. geometrica, T.* sp.
„ *microcephala* Rud.	*Ardea cinerea.*
„ *rosmari* Baylis (=*A. bicolor* Baird)	*Odobaenus rosmarus.*
„ *semiteres* (Zed.)	*Vanellus cristatus.*
„ *serpentulus* Rud. (?=*A. ardeae* Froel.)	*Ardea cinerea.*
„ *similis* Baird	A seal (Antarctic).
Contracaecum spiculigerum (Rud.)	*Phalacrocorax verrucosus, P. campbelli, P.* sp.
Dujardinia helicina (Molin)	*Crocodilus niloticus.*
Kathleena osculata (Rud.)	*Hydrurga leptonyx.*
„ *radiata* (v. Linst.)	*Leptonychotes weddelli.*
„ *rodhaini* Gedoelst	*Plotus rufus.*
„ *tricuspis* Gedoelst	*Phalacrocorax africana.*
Porrocaecum crassum (Deslongchamps)	*Anas boscas dom.*
Terranova antarctica Leiper and Atkinson	*Mustelus antarcticus.*

Among the forms just enumerated, the hosts of which include mammals, birds, reptiles and fishes, no example of the typical, simple, Ascarid structure of the alimentary canal was met with. In every case some modification of the oesophagus was present, or some caecum or appendage either of the oesophagus or of the intestine, or both.

Five main types of structure were encountered:

I. Oesophagus muscular throughout, opening directly into the intestine, without posterior ventriculus or distinct bulb. A forwardly-directed caecum springs from the intestine. No oesophageal appendix. Examples: *Ascaris holoptera, A. colura.*

II. Oesophagus slender, with a more or less distinct globular bulb at the base. The intestine is produced forwards as a long caecum. No oesophageal appendix. Examples: *Ascaris halichoris, Dujardinia helicina.*

III. Oesophagus with a posterior glandular portion, or ventriculus, of elongate or oblong shape and often bent in a sigmoid manner. No oesophageal or intestinal caeca. Examples: *Ascaris rosmari, A. similis.*

[1] The determination cannot in all cases be vouched for with certainty, though no undue suspicion attaches to any of the specimens. Those of *Ascaris colura, A. rosmari, A. similis* and *Terranova antarctica* are the type-specimens of the species in question. Those of *Kathleena osculata* and *K. radiata* were determined by Leiper and Atkinson, being part of the "Terra Nova" collection. The examples of *A. decipiens* had been misdetermined by von Linstow as "*A. simplex* Rud.," and the present determination is the writer's. Two out of the three sets of *C. spiculigerum* (*Ascaris spiculigera* Rud.), belonging to the "Challenger" and "Discovery" collections respectively, were determined by von Linstow. Named specimens of *Porrocaecum crassum* were kindly supplied by Prof. Railliet.

IV. Oesophagus with a posterior glandular portion, or ventriculus, often bent so as to open into the intestine laterally. An intestinal caecum present. No oesophageal appendix. Examples: *Ascaris decipiens, A. depressa, A. ensicaudata, Porrocaecum crassum, Terranova antarctica,* probably *Ascaris semiteres, A. serpentulus*[1].

V. Oesophagus with a reduced posterior ventriculus, giving off a backwardly-directed glandular appendix. An intestinal caecum also present. Examples: *Ascaris aucta, A. microcephala, Contracaecum spiculigerum, Kathleena osculata, K. radiata, K. rodhaini, K. tricuspis.*

The subfamily Heterocheilinae, Railliet and Henry.

We may next consider the classification outlined by Railliet and Henry (1912), to which reference has already been made. These authors divided the family Ascaridae into the following subfamilies:

(1) Ascarinae, to include *Ascaris* L. and other genera with a simple alimentary canal.

(2) Anisakinae, to include *Anisakis* Duj., 1845 (= *Peritrachelius* Dies., 1851; = *Conocephalus* Dies., 1861) and perhaps *Crossocephalus* Railliet, 1909 (= *Pterocephalus* v. Linst., 1899).

(3) Heterocheilinae, to include provisionally all the forms with oesophageal or intestinal caeca. *Heterocheilus* Dies., 1839; *Typhlophorus* v. Linst., 1906; *Porrocaecum* Railliet and Henry, 1912; *Crossophorus* Hempr. and Ehbr., 1828; *Lecanocephalus* Dies., 1839; *Contracaecum* Railliet and Henry, 1912. To these were subsequently added (1915) the genera *Terranova* and *Kathleena* of Leiper and Atkinson, 1914, and *Raphidascaris* Railliet and Henry, 1915.

With the first subfamily it is not intended to deal at present. Of the forms included in the last two subfamilies, it is important to note the following features.

Anisakis (type-species (?) "*Ascaris simplex* Rud." of Dujardin—type-specimens renamed *A. dussumieri* by van Beneden, 1870—? synonym, *Peritrachelius* [*Conocephalus*] *typicus* (Dies., 1860); Host, *Delphinus*). The main character upon which Dujardin's subgenus *Anisakis* was based was the presence of two spicules of unequal length in the male. The descriptions of *A. dussumieri* and of *Ascaris* [*Peritrachelius*] *typica* show, however, that the oesophagus possesses a posterior ventriculus of different histological appearance from the anterior, muscular portion, and that oesophageal and intestinal caeca are absent. (See Stiles and Hassall (1899), where the anatomy and the complicated synonymy are fully dealt with.)

Crossocephalus, as more recent researches (Gedoelst (1916); Baylis (1919, *a*))

[1] The material available for the study of the last two forms did not permit of satisfactory examination.

have shown, has no close relationship with any of the Ascaridae, and probably belongs to the Oxyuridae.

Heterocheilus (type-species, *H. tunicatus* Dies., 1839, from *Manatus exunguis*) has a very peculiar cuticular swelling behind the lips, consisting of a series of longitudinal ribs; while the lips themselves, from Diesing's figures, seem to be of an unusual type. The oesophagus has a bulb at the base, and there is an intestinal caecum running forwards.

Typhlophorus (type-species, *T. lamellaris* v. Linst., 1906, from *Gavialis gangeticus*). From the brief description of this form, and from the figures, it appears to be closely related to *Heterocheilus*. There is a very similar longitudinally-ribbed cuticular swelling behind the lips. A long intestinal caecum is present, but the structure of the oesophagus is not described.

Porrocaecum (type-species, *P.* [*Ascaris*] *crassum* (Deslongchamps), from ducks). In the structure of the alimentary canal this genus corresponds to Dujardin's Section 2, which includes the type-species, and also to what has just now been described as "type IV."

Crossophorus is a genus of so highly specialised a type that it seems to have little or nothing in common with the other genera. It certainly possesses two long intestinal caeca, but in several features (see Baylis (1919, *b*)) it appears to be quite isolated.

Lecanocephalus. The correct generic name, as Railliet and Henry (1915) have pointed out, is *Goezia* Zeder, 1800 (type-species, *G. ascaroides* (Goeze, 1782), from *Silurus glanis*). This genus is characterised by having the cuticle armed with numerous transverse rings of spines, and by the peculiar, flattened shape of the lips, which are unlike those of any other known Ascarid. For these reasons it may be doubted whether it bears any close relationship to most of the genera among which it has been placed. Its claim to this position is based on its possession of a long glandular oesophageal appendix and a short intestinal caecum, in which respects it resembles *Contracaecum.*

Contracaecum (type-species, *C.* [*Ascaris*] *spiculigerum* (Rud., 1809), from the cormorant, etc.) corresponds, in the structure of the alimentary canal, to Dujardin's Section 3, and to "type V" in the list given above.

Terranova (type-species, *T. antarctica* Leiper and Atkinson, 1914, from a shark, *Mustelus antarcticus*). The characters upon which this genus was based were "three large simple lips. No interlabia. Oesophagus simple. Gut with anterior caecal prolongation. No oesophageal appendage." A re-examination of the type-specimen, however, shows that the statement that the oesophagus is simple was erroneous, and that, on the contrary, it has a specialised ventricular portion, 1·4 mm. long, and therefore the structure is of the same type as in *Porrocaecum.*

Kathleena (type-species, *K. osculata* (Rud., 1802), from seals). On comparing examples of the two type-species, the characters of this genus appear to be identical with those of *Contracaecum.*

Raphidascaris (type-species, *R. acus* (Bloch, 1779), from the pike) is

characterised by the possession of an oesophageal appendix, but no intestinal caecum.

From this survey it appears doubtful whether the subfamily Heterocheilinae, as it stands, can be regarded as a satisfactory or natural group. We have seen that *Crossophorus* probably ought to be removed to a position by itself. The genera *Heterocheilus*, *Typhlophorus* and *Goezia* (= *Lecanocephalus*) also seem to be clearly marked off from the rest of the forms by peculiarities of external features—all the remainder being of typical "Ascarid" appearance externally.

There can be little question that *Terranova* is generically identical with *Porrocaecum*, and *Kathleena* with *Contracaecum*. Hence, according to the law of priority, the names *Terranova* and *Kathleena* fall into synonymy.

Setting aside all the aberrant forms mentioned above, the only genera among the original Heterocheilinae with which we are immediately concerned are *Porrocaecum*, *Contracaecum* and *Raphidascaris*. These genera, together with *Anisakis*, and with the addition of certain other forms to be mentioned, seem to compose a more natural group, united by possessing the general outward appearance of an "Ascaris," but with certain modifications of the alimentary canal which mark them off from the Ascarinae.

Proposed new arrangement.

The new group which it is proposed to set up comprises the type-genus of the former subfamily Anisakinae and part of the former subfamily Heterocheilinae. The forms which are to be included in it may be divided into two sections, according to the presence or absence of a specialised "ventriculus," forming a posterior division of the oesophagus. This structure, for which Dujardin's term may conveniently be used, has been neglected since his time as a feature of systematic value. It seems to the writer, however, that it deserves the consideration which Dujardin was disposed to give to it, and that it is probably of greater phylogenetic importance than the presence or absence of caecal appendages. Although no special attention has as yet been devoted to the ventriculus of Ascarids from the histological or physiological standpoints, it is interesting to observe that in a nematode of another family, *Camallanus*, in which a very similar organ exists, a recent writer (Magath (1919)) has suggested that it is concerned in the excretory processes. In the species dealt with it seems to have some structural connection with the excretory apparatus. Now in some of the Ascarids in which a ventriculus occurs we find it associated with a peculiar type of excretory apparatus, terminating in a long, unpaired, unicellular "gland," opening close to the lips. This is the case, at all events, with a number of the forms included here under the names *Anisakis*, *Porrocaecum* and *Contracaecum*, and will very possibly be found to be characteristic of all the forms in which there is a ventriculus. Pending fuller investigation, therefore, it is suggested that all

the forms with a true ventriculus should be placed together. It may prove that the forms without a true ventriculus ought to be entirely separated from those possessing it, and that their inclusion in the same subfamily is too artificial. Certain forms of this type may, however, be placed here at present provisionally. The true relationships of all the genera and species can, of course, only be estimated after a much fuller inquiry into their entire anatomy.

The following arrangement is suggested:

ANISAKINAE Railliet and Henry, 1912, *emend.* Baylis, 1920.

Ascaridae having the general external appearance of an *Ascaris*, *i.e.* with a smooth cuticle, transversely striated but without cuticular spines or other raised structures. The oesophagus may or may not be divided into an anterior muscular portion and a posterior ventriculus of different histological structure. When the latter is absent (and frequently when it is present) there is an anterior caecum, springing from the intestine and lying alongside of the oesophagus. A posterior caecum or solid glandular appendix may also be developed in connection with the ventricular portion of the oesophagus. Interlabia may be present or absent, and when present show various degrees of development. Dentigerous ridges on the lips may also be present or absent. The species are parasitic in the alimentary canal of mammals, birds, reptiles and fishes, and the majority are found in aquatic or at least fish-eating hosts. There is reason to believe that in some cases, and perhaps in all, an intermediate host is required for their development, and that, in the case of species inhabiting fish-eating animals when adult, the intermediate host is a fish.

Type-genus—*Anisakis* Duj., 1845.

The following genera may be enumerated:

(1) *Anisakis* Duj., 1845 [= *Peritrachelius* Dies., 1851; = *Conocephalus* Dies., 1861].

Oesophagus with anterior muscular portion and posterior ventriculus, the latter being oblong or sigmoid in shape. No oesophageal or intestinal caecum. Interlabia absent. Dentigerous ridges present. Spicules of male sometimes unequal.

Hab.—stomach and intestine of marine mammals.

With the following species:

A. dussumieri van Ben., 1870 (=*A. simplex* Duj., 1845, *nec* Rudolphi, 1809) (genotype) from a dolphin.

A. typica (Dies., 1860) from *Delphinus, Phocaena, Prodelphinus* (perhaps identical with the preceding).

A. insignis (Dies., 1851) from *Inia geoffroyi* (=*Delphinus amazonicus*).

A. similis (Baird, 1853) from a seal (Antarctic).

A. rosmari (Baylis, 1916) [=*Ascaris bicolor* Baird, 1868] from the Walrus (*Odobaenus rosmarus*).

A. simplex (Rud. 1809) from *Balaenoptera, Delphinus*, etc.

?*A. kükenthalii* (Cobb, 1888) from *Delphinapterus* (sp. inq.; perhaps=*A. simplex*).

(2) *Raphidascaris* Railliet and Henry, 1915[1].

Oesophagus with anterior muscular portion and small posterior ventriculus. From the latter springs a small posterior appendix. No intestinal caecum. Interlabia present. Dentigerous ridges absent.

Hab.—intestine and stomach of fishes.

Species:

R. acus (Bloch, 1779) (genotype) from the pike (*Esox*).

(3) *Porrocaecum* Railliet and Henry, 1912. (Syn. *Terranova* Leiper and Atkinson, 1914.)

Oesophagus with anterior muscular portion and posterior ventriculus of oblong shape, the latter short in the genotype, but in other species frequently long and bent at an angle so as to open into the intestine laterally. An intestinal caecum present. No oesophageal appendix. Interlabia present, usually small. Dentigerous ridges present.

Hab.—intestine of birds, marine mammals and fishes.

Species:

P. crassum (Deslongchamps, 1824) (genotype) from ducks.
P. depressum (Zed., 1800) from birds of prey (*Falco*, etc.).
P. ensicaudatum (Zed., 1800)[2] from *Turdus*, *Sturnus*.
P. decipiens (Krabbe, 1878) from seals.
P. antarcticum (Leiper and Atkinson, 1914) from *Mustelus antarcticus*, and probably also
P. semiteres (Zed., 1800)[3] from *Vanellus*, etc.
P. serpentulus (Rud., 1809) from *Ardea* sp.
P. heteroura (Crepl., 1829) from *Charadrius*, etc.
P. spirale (Zed , 1803) from owls.
P. praelongum (Duj., 1845) from *Colymbus*.

Certain species from fishes, with this type of alimentary canal, mentioned by Dujardin, require further investigation.

(4) *Contracaecum* Railliet and Henry, 1912. (Syn. *Kathleena* Leiper and Atkinson, 1914.)

Oesophagus with reduced posterior ventriculus, giving off a solid posterior appendix. An intestinal caecum present. Interlabia present, usually very well-developed. Dentigerous ridges absent[4].

[1] Ward and Magath (1916) have described a new genus, *Hysterothylacium* (type-species *H. brachyurum* Ward and Magath, from the "black bass"), which is stated to belong to the Heterocheilidae and to have the following characters: "Esophagus long, slender, with terminal spherical bulb. Intestine with short simple cecum, arising from anterior end of intestine, directed posteriad." The oesophageal bulb is said to contain three teeth. The authors do not make any comparison between this form and *Raphidascaris*, but it appears not unlikely that the two forms are related. It is important to note, however, that the caecum is said to belong to the intestine and not to the oesophagus. Wigdor (1918) has described a second species, *H. cayugensis*, from *Esox* and *Ameiurus*, which, from its description, can hardly be distinguished from *Raphidascaris acus*.

[2] In *P. ensicaudatum* the caecum is very small and almost rudimentary, at least in the examples seen.

[3] The single specimen of *P. semiteres* available for study proved too opaque for the structure to be made out with certainty.

[4] Gedoelst's (1916) statement that dentigerous ridges are present in *Contracaecum* is ap-

Hab.—intestine of fish-eating mammals and birds, and of fishes.

Species:

C. spiculigerum (Rud., 1809) (genotype) from cormorants, etc.
C. osculatum (Rud., 1802) from seals.
C. radiatum (v. Linst., 1906) from seals.
C. rectangulum (v. Linst., 1906) from seals.
C. scotti (Leiper and Atkinson, 1914) from *Diomedea*.
C. microcephalum (Rud., 1809) from *Ardea*, etc.
C. rodhaini (Gedoelst, 1916) from *Plotus rufus*.
C. auctum (Rud., 1809)[1] from *Blennius*, etc.
C. clavatum (Rud., 1819) from various fishes.
C. aduncum (Rud., 1809) from *Clupea*.

And probably other species from fishes (see Dujardin (1845), pp. 208–211).

Gedoelst (1916) has compiled a list of species to be referred to *Kathleena*. These should probably all be included here, and we have therefore the following additional species:

C. lobulatum (Schneider, 1866) from *Platanista gangetica*.
C. falcigerum (Railliet and Henry, 1907) from seals.
C. multipapillatum (v. Drasche, 1882) from *Tantalus loculator*.
C. micropapillatum (Stossich,1890) from *Pelecanus* spp.
C. ovale (v. Linst., 1907) from *Podiceps cristatus*.
C. rosarium (Connal, 1912) from *Nycticorax* sp.
C. tricuspe (Gedoelst, 1916) from *Ardea* sp.
C. punctatum (Gedoelst, 1916) from ?*Pseudotantalus ibis*.

Kathleena arcuata Gedoelst, 1916, from *Ardea*, sp., appears to the writer to be identical with *C. microcephalum* (Rud.).

(5) *Dujardinia* Gedoelst, 1916.

Oesophagus with a small posterior spherical bulb. An intestinal caecum present. No oesophageal appendix. Interlabia present. Dentigerous ridges absent.

Species:

D. helicina (Molin, 1860) (genotype) from *Crocodilus* spp.
D. halichoris (Owen, 1833) from *Dugong* spp.

(6) *Angusticaecum*, n.g.

Oesophagus without ventriculus or distinct bulb. A long slender caecum springs from the intestine a little behind its origin. No oesophageal appendix. Interlabia absent. Dentigerous ridges present.

Species:

A. holopterum (Rud., 1819) (genotype) from *Testudo* spp.
A. [*Porrocaecum*] *numidicum* (Seurat, 1917) from *Rana ridibunda*.

(7) *Amplicaecum*, n.g.

Oesophagus without ventriculus or distinct bulb. A wide intestinal caecum

parently an error. They have not been observed in the species examined, and the distinction between *Contracaecum* and *Kathleena*, based on this point, does not appear to hold good.

[1] *C. auctum* has the interlabia much reduced.

present. No oesophageal appendix. Small interlabia present. Dentigerous ridges present.

Species:

A. colurum (Baylis, 1919) (genotype) from *Lophoaëtus occipitalis*.

A table may now be given which will serve to distinguish the genera mentioned, and also show to some extent the relationships supposed to exist between them.

A. Oesophagus divided into an anterior muscular portion and a posterior ventriculus, the latter being oblong or sigmoid in shape, or having a posterior appendix.

(*a*) An intestinal caecum present.

(α) An oesophageal appendix present...*Contracaecum*.
(β) Oesophageal appendix absent...*Porrocaecum*.

(*b*) No intestinal caecum.

(α) An oesophageal appendix present...*Raphidascaris*.
(β) Oesophageal appendix absent...*Anisakis*.

B. Oesophagus without ventriculus, with or without a small but distinct posterior bulb. The latter, if present, spherical and without a posterior appendix. An intestinal caecum present.

(*a*) A distinct spherical oesophageal bulb present...*Dujardinia*.

(*b*) Distinct oesophageal bulb absent.

(α) Small interlabia present...*Amplicaecum*.
(β) Interlabia absent...*Angusticaecum*.

We have now to consider the position of the genera which were removed from the rest of the "Heterocheilinae"—*Heterocheilus*, *Typhlophorus*, *Goezia* and *Crossophorus*. The last-named genus seems so unlike any other Ascarid at present known that it may at once be placed in a subfamily by itself, which may be called CROSSOPHORINAE, n. subfam.

As regards the remaining three genera, it may be well to recall that von Drasche (1884) placed *Lecanocephalus* (= *Goezia*) and *Heterocheilus* in separate categories, which he named Lecanocephalidea and Heterocheilidea respectively. Considering the peculiarities of the genera in question, it seems not unreasonable to retain von Drasche's arrangement, and altering his names in accordance with the plan of modern nomenclature, to place *Heterocheilus* and *Typhlophorus* together in a subfamily HETEROCHEILINAE (or, in other words, to restrict Railliet and Henry's (1912) subfamily to these two genera), and *Goezia* by itself in another subfamily, GOEZIINAE.

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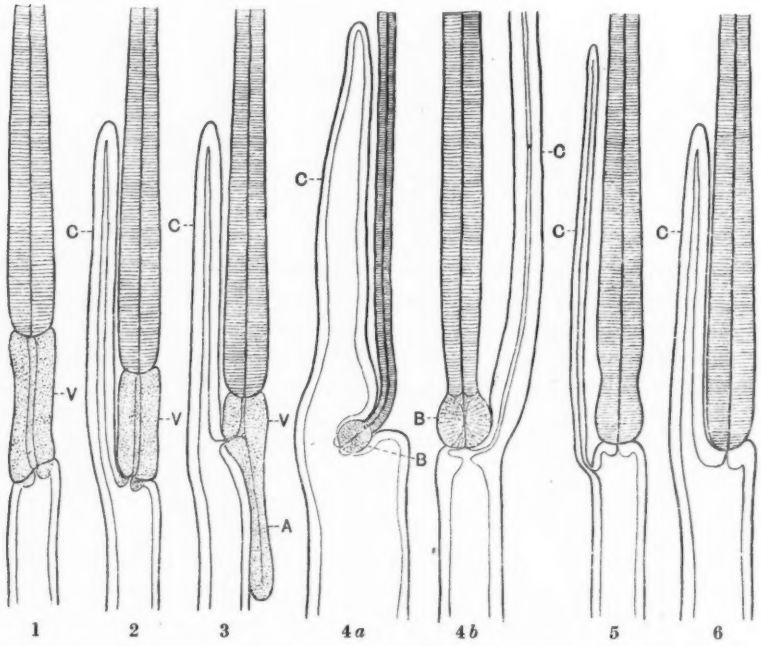

A series of diagrams illustrating certain types of structure met with in the alimentary canal of Ascaridae. The shaded portion represents the hinder part of the oesophagus.

A, oesophageal appendix; B, oesophageal bulb; C, intestinal caecum; V, ventriculus.

1, *Anisakis*; 2, *Porrocaecum*; 3, *Contracaecum*; 4, *Dujardinia* (4*a*, *D. helicina*; 4*b*, *D. halichoris*); 5, *Angusticaecum*; 6, *Amplicaecum.*

No specimens of *Raphidascaris* having been available, the structure found in this genus has not been figured. It is presumably like (3), but without the intestinal caecum.

SARCOPTIC SCABIES IN MAN AND ANIMALS.

A CRITICAL SURVEY OF OUR PRESENT KNOWLEDGE REGARDING THE ACARI CONCERNED[1].

By CECIL WARBURTON, M.A., F.Z.S.,

Demonstrator in Medical Entomology, etc., in the University of Cambridge.

(*From the Quick Laboratory, Cambridge.*)

(With Plate XV and 10 Text-figures.)

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INTRODUCTION.

Sarcoptic scabies in man and in domestic and wild mammals has engaged the attention of a large number of investigators since its true nature was finally established about the year 1835. The subject has been approached from the medical, the veterinary and the entomological side, and the literature concerning it has attained very large dimensions. Nevertheless it cannot be said that our knowledge of the matter is in a satisfactory condition, since no two writers agree entirely in their accounts of the morphology and bionomics of the human itch-mite, and the most diverse views are held as to the interrelation of the forms which infest man and the lower animals.

Munro (1919) goes so far as to say that "no satisfactory description of any of the members of the genus *Sarcoptes* has yet been given." If this be so it is not for want of patient investigation by a number of scientific men exceedingly well equipped for the task, but the creatures concerned are so small and so slightly chitinised, and the minute differences between them are

[1] Work done with the aid of a grant from the Ministry of Agriculture and Fisheries.

so difficult of observation that their thorough investigation is a matter of great intrinsic difficulty.

A revision of the subject is urgently needed, with the examination of fresh material, and a full knowledge of the results obtained hitherto. Such a revision will be greatly facilitated if the conclusions of previous workers are collated and presented in a compact form, and their chief discrepancies clearly indicated, and this is the immediate object of the present article.

HISTORICAL.

Real knowledge concerning the nature and cause of scabies dates from the 16th century. Numerous passages in the writings of the ancients seem to prove an acquaintance with the disease, which has no doubt afflicted man and domestic animals from time immemorial, but until the various skin diseases were discriminated and the parasites to which some of them are attributable had been discovered and studied, such allusions were bound to be vague and unsatisfactory.

Scaliger (1557) is the first writer to show an exact knowledge of the subject. He describes how the parasite "lodges under the epidermis and burns by the galleries it burrows." Ambroise Paré (1564) explains how the mites can be extracted by the aid of a needle. Aldrovandus (1596) gives an unmistakeable account of the disease, so that it is clear that much accurate information on the matter existed by the end of the 16th century.

Further progress was made during the 17th century. The Englishman Thomas Moffett (or Muffet, Moufet, Moufetius) (1634) states that the mites do not inhabit the pustules but are to be found near-by—an observation which would have saved much trouble if subsequent investigators had borne it in mind—and Hauptmann (1657), in a work on the Waters of Wolkenstein, gave for the first time a (very inaccurate) figure of the parasite.

Then Bonomo[1] (perhaps a pseudonym for Cestoni), in a letter to Redi written in 1687, treated the subject in a manner remarkable for its admixture of truth and error, and his figure held the field till the middle of the next century as the classical representation of the sarcopt, being given a new lease of life by its use by Mead in *Philosophical Transactions* for 1702. So the matter rested till the advent of Linnaeus, who gave a good account of the mite and its habits, though he vacillated with regard to its name and systematic position, calling it *Acarus humanus subcutaneous* (1734) and *Acarus scabiei* with a doubtfully distinct form *Acarus exulcerans* parasitic on animals (1758), but to the end confusing it with the flour-mite *Tyroglyphus*.

The first thorough-going study of the mite as the exclusive cause of scabies is that of De Geer (1778), and in 1786 the Hanoverian physician

[1] The letter to Redi was signed Giovan. Cosimo Bonomo. Delafond and Bourguignon (p. 89) say roundly that Cestoni wrote to Redi under this pseudonym, and their contemporaries were of the same opinion. There was, however, a Dr Cosimo Bonomo who was a pupil of and a collaborator with Cestoni. The matter is fully discussed in Fürstenberg, p. 13 *et seq.*

Wichmann[1] published his *Aetiologie der Krätze*, giving an excellent account of scabies and its cause, supported by several new observations. Then sundry writers (Pinel on the medical side and Latreille on the entomological side) took up a discussion on the systematic position of the mite, trusting to the figures of Cestoni and De Geer. Latreille founded the genus *Sarcoptes* in 1806.

The history of the subject during the early years of the 19th century is most curious. Various medical writers (Alibert, 1833; Biett, 1836; and others), overlooking Moffett's observation and examining only the vesicles and pustules, declared that they were quite unable to find the mite in numerous undoubted cases of scabies. Galès, indeed, described and figured (1812) a mite which he said inhabited the pustules, but others could not find it, and by many this re-discovery was regarded as an imposture, and in 1821 Mouronval published a volume to prove that it did not exist!

Meanwhile Walz (1809) had been investigating sheep scabies, and de St Didier (1813) and Gohier (1816) had studied horse scabies, but the doctors remained ignorant of the work done by the veterinarians.

Then Raspail attempted a revision of the whole matter as regards human scabies, and his statement that the mite found by Galès was the cheese mite, aroused great interest, and all concerned became eager to have the matter settled once for all. At this time Francis Renucci, a Corsican, accustomed from his infancy to the "chasse aux sarcoptes," was studying medicine in Paris, and had no difficulty at all in proving the existence of the mite. This re-discovery was communicated to Raspail who published (1834) a *Mémoire comparatif sur l'histoire de l'insecte de la Gale*, which, however, contained many errors. In the same year Albin Gras published a much better account of the *Sarcoptes*, and in 1835 Renucci himself presented his thesis for the doctorate with figures of the *Sarcoptes* of man, the horse, the sheep and the cat, and also a figure of the cheese mite.

This was the condition of things when in 1843 Bourguignon, who was at the Veterinary College at Alfort under Prof. Delafond, undertook his admirable study of human scabies. He handed in his *Traité entomologique* in 1846, but it was not published till 1852. Meanwhile Hebra was at work in Vienna, and Eichstedt in Germany. Bourguignon does not seem to have known of Eichstedt's work, which included a remarkably fine study of the galleries of *Sarcoptes*, the arrangement of the eggs in them, the phenomena of moulting etc., but he had some acquaintance with Hebra's investigations, and questions of priority arose in 1845 between Hebra and Bourguignon. Of this period also is the work by Gurlt and Hertwig on human scabies (1844).

The nature and cause of scabies was now firmly established and generally admitted, but there was much to be discovered, and a large number of students were attracted to a field in which so much interest had been aroused. Scabies

[1] According to Raspail, Wichmann's treatise is a little 12mo. volume sometimes to be found bound up with a treatise by Guldner on the Prague workhouse. This is the second edition, published 1791.

became quite fashionable as a subject for theses for the doctorate. Gerlach published his *Krätze und Räude* in 1857; Fürstenberg his *Krätzmilben der Menschen und Thiere* in 1861; and Delafond and Bourguignon their *Traité pratique* in 1862.

The fine works of Bourguignon, Gerlach and Fürstenberg are generally regarded as the classical publications on this subject, and deserve a special notice. They present a remarkable variety of style and outlook.

Bourguignon is a leisurely, elegant, philosophical—and it must be confessed sometimes prolix—writer, who works away patiently and indefatigably, without too much reference to what his contemporaries are doing, though he is learned on the ancient history of the subject. He anticipates incredulity for some of his results, but is prepared to stand by them. "Tous les faits que nous avançons ont été vus cent fois avant d'être définitivement admis, et comme beaucoup d'entre eux échapperont nécessairement au premier abord aux entomologistes, qui seraient tentés de les vérifier, car la grande habitude d'étudier le même objet vous donne à la longue une habileté, qu'on n'aurait pas dans le principe serait-on le plus habile des observateurs, nous prions ceux, qui contesteraient la présence de tel ou tel organe, de nous permettre de leur fournir la preuve de son existence" (*Traité entomologique*, p. 15). One cannot "say fairer" than that!

He pays much attention to the dorsal armature, and to the skeletal structure of the legs and rostrum. He found and described the male, and observed the tocostome of the female, and altogether did remarkable pioneer work, though his details have in many respects been proved to be inaccurate by subsequent observers with more adequate instruments.

His joint work with Delafond—the *Traité pratique*, published in 1862—is a comprehensive account of scabies—whether sarcoptic, psoroptic or chorioptic—on man and other animals as known at that date. It is divided (like Gaul) into three parts. Part I deals with classification, anatomy and development, and physiology. Part II deals with scabies in man, lemur, bear, hyaena, fox, dog, lion, cat, wombat, llama, sheep, ox and fowl. Its main theme is that carnivorous and omnivorous animals (bear, dog, hyaena, lion, cat, pig) are subject to a form of scabies transmissible to man, due to a *Sarcoptes* which is probably identical with man's; and that herbivorous animals (horse, camel, llama, sheep) *may* have a *Sarcoptès* and transmit it to man, but that they are more subject to psoroptic and chorioptic scabies not so transmissible. Part III is medical, and deals with treatment.

Bourguignon made many experiments in transferring *Sarcoptes* from one animal to another, and in several passages he calls attention to what he believes is the peculiar position held by man with regard to these mites. Thus on p. 613 of the *Traité pratique* he says: "Man has the sad privilege of being free from the law which regulates all contagion of animals among themselves. His skin always offers an asylum suitable for *Sarcoptes*; his dermal fluids are always to their taste, and there is to-day no doubt that the

true cause of man's persistent scabies exists, not in contagion between diseased and healthy man, but in the frequent transmission of this disease to man by animals."

Gerlach's treatise is important (for our purpose) chiefly for its study of the horse *Sarcoptes* and its comparison with that of man, and for his description and figures of the *Sarcoptes* of the dog and the pig. He gives a figure of the burrow or gallery of the human itch-mite (very adversely criticised by Delafond and Bourguignon) and in some respects his illustrations are among the best, if minute detail be not looked for.

Out of 230 folio pages of Fürstenberg's remarkable work no fewer than 170 are occupied by a truly wonderful digest of the writings of every author, from Aristotle downwards, who had hitherto dealt with the subject. The portion of the treatise which especially concerns us is not extensive, but it is extremely important because of the minute detail with which the skeletal tissues and the armature of scales and spines are dealt with, the figures being drawn by aid of a "camera clara" of his own construction. Some of his drawings of dorsal scales and cones are magnified 700 times. Nevertheless in many of his figures he makes the extraordinary mistake of giving his *Sarcoptes* two pairs of chelicerae!

Of subsequent writers two of the most important are Robin who in 1869 published his *Mémoires sur diverses espèces d'Acariens de la Famille des Sarcoptidés*, and Mégnin, who, among numerous brochures on the Acarina, contributed several which dealt especially with this group.

All the writers of compendia on parasitology of a later date (L. G. Neumann, Blanchard, Railliet, Brumpt, Neveu-Lemaire, etc.) have necessarily dealt with the subject as far as the scope of their work permitted, and some of them, notably Railliet, have made original contributions to our knowledge. From a purely medical point of view the literature has become immense, but with this aspect of the matter we are not here especially concerned.

CLASSIFICATION AND MORPHOLOGY OF THE SARCOPTINAE.

There is as yet no generally accepted classification of the Acarina. Very much work has been done of recent years in certain groups, and a few have been monographed. There is, indeed, substantial agreement as to the general affinities of the various members of the order, but the widest differences exist as to the rank to be attributed to its subdivisions. Thus while Canestrini (*Atti Ist. Veneto*, II. 1891) admitted 34 families, Trouessart (*Rev. Sci. Nat. Ouest*, II. 1892) allowed only ten.

To come at once to the group with which we are especially concerned, the term Sarcoptidae has quite a different scope as employed by different systematists. Canestrini and Kramer (Schultze's *Tierreich*, 1899) use it in the widest sense, making it equivalent to what Banks (1904) and others regard as the super family Sarcoptoidea, while their Sarcoptinae are the whole family of Sarcoptidae as understood by the latter school, and include the following

genera: *Sarcoptes, Notoedres, Prosopodectes, Cnemidocoptes, Psoroptes, Psoralges, Chorioptes, Caparinia, Otodectes.* This view is far from satisfactory as it takes no account of the specially close affinity between the four first-named genera, which agree in possessing mouth-parts adapted for burrowing, and are, in fact, the forms which induce "sarcoptic scabies" in various animals. It is much more convenient, and, indeed, is the general practice, to consider the nine genera above named as constituting the SARCOPTIDAE, of which a subfamily SARCOPTINAE includes the four genera *Sarcoptes, Notoedres, Prosopodectes* and *Cnemidocoptes*, and it is with the Sarcoptinae in this restricted sense that we are concerned. *Prosopodectes* is a parasite only found in the ears of bats, and it is not proposed to discuss it, so that only three genera remain. Indeed since *Cnemidocoptes* is parasitic only on birds, our chief interest is in the genera *Sarcoptes* and *Notoedres.*

Sarcoptes, Notoedres and *Cnemidocoptes* are precisely the *Sarcoptes communes, Sarcoptes notoèdres* and *Sarcoptes anacanthes* of Delafond and Bourguignon (1862, p. 13).

SARCOPTES Latreille, 1806.

The *Tierreich* definition is: ♂ without anal cylinders (Analnäpfe), ♀ without copulation tubes; long unjointed ambulacra on the two anterior legs of the ♀ and the two anterior and the second posterior legs of the ♂. Anus terminal. Oviparous parasites of mammalia.

Berlese (*Acarotheca italica*, Textus, 1913) thus defines the genus:

Maris disculi copulationis foeminaeque tuberculi nulli. Ambulacra longe pedunculata, pedunculo haud articulato, in foemina sunt in pedibus primi secundique paris, in mari in primo secundo quartoque pari. Anus in margine postico abdominis apertus. Ovipari, mammalicoli, scabiem sarcopticam inducentes. Species typica *Acarus scabiei* De Geer. Totus mundus.

He admits 15 species, namely: *scabiei* De G., *canis* Gerl., *caprae* Fürst., *dromedarii* Gerv., *equi* Gerl., *ovis* Mégn., *parvulus* Can., *cuniculi* Neum., *scabiei-crustosae* Fürst., *suis* Gerl., *vulpis* Fürst., *aucheniae* Raill., *hydrochaeri* Mégn., *rupicaprae* Hering, *wombati* Raill.

Canestrini and Kramer (in Schultze's *Tierreich*, 1899) include all these together with three others, *leonis* Can., *lupi* Mégn., *furonis* Raill., in their list of species, but they consider *aucheniae, hydrochaeri, rupicaprae* and *wombati* "doubtful."

And now it will be as well to interpose at the outset the gist of a passage from Mégnin (1875, pp. 1058–1060) so significant that it is bound to affect profoundly the views of anyone engaged on a revision of the matter. He had been studying the *Sarcoptes* of the horse during and after the Franco-Prussian War (1871 and 1872), and had created a new species, *S. uncinatus*, based on:

(1) the presence of a strong claw on the inferior face of the second article of each anterior leg;

(2) the presence in the middle of the notothorax in both sexes, but

stronger in the ♂, of a quadrangular, chitinous, granular, yellowish "plastron," presenting in the middle of its anterior border two rudiments of stigmata;

(3) the presence, on the notogaster of the ♂, of two chitinous, granular, yellowish, circular, symmetrical plates between the four rows of spinules.

Continuing his studies on *Sarcoptes* collected by himself from the giraffe, gazelle, wolf etc., and on specimens furnished him by Gervais from the llama, moufflon, cabiai etc., he found in them precisely the same details of structure. Finally, on examining specimens taken from patients at the hospital of St Louis he was again able to recognise the characteristics he had thought peculiar to his new species on the horse, but so indistinct and colourless that they were not noticeable until especially looked for. His conclusion is that the "German authors" have depended on habitat and insignificant characters in founding a large number of species, while there is in reality only one species —*S. scabiei*, with a certain number of varieties. He finally remarks: "The different varieties are characterised by a difference of activity in their poisonous buccal liquid. I have just recently placed on the horse the *Sarcoptes* taken from the wolf, and they gave rise to colonies which *in ten days* invaded the whole surface of the pachyderm, giving rise to a scabies much more severe than that caused by its own proper *Sarcoptes*!"

This passage, be it remarked, long antedated the works cited above in which authors of such undoubted authority as Kramer, Canestrini and Berlese give extensive lists of distinct species of *Sarcoptes*.

The plan which seems best adapted to our purpose is to give in the first place a full account of the *Sarcoptes* of man as far as it is known, indicating differences of opinion where they exist, and then to deal briefly with the forms which affect other animals. Many of the latter are occasionally to be found on man, but it is usually easy to trace the circumstances of contagion from definite mangy animals, whereas the disease of scabies which exists year after year in the poorer and more crowded parts of our cities is held to be due to the particular form—whether species, variety or race—known as *Sarcoptes scabiei* De Geer. Delafond and Bourguignon, indeed, state their opinion (1862, p. 102) that if human scabies depended entirely on successive generations from man to man it would have been stamped out long ago, because so easy to treat, but that it is reinforced from domestic animals; and again (p. 142) they say "Man seems rather to have the Sarcoptes and the Scabies of animals than a Sarcoptes and a Scabies peculiar to the human species." But whatever truth there may be in this, it is certainly the case that one form of *Sarcoptes*, in default of treatment, is perfectly at home on mankind, and can maintain its ground for an indefinite period without any reinforcement from other sources, and has come to be regarded as *par excellence* the *Sarcoptes* of man.

Incidentally it may be remarked that the same two investigators (D. and B.) insist on a remarkable difference between man and other animals, as the hosts of *Sarcoptes*. In other animals, they say, a certain "predisposition" is

necessary if the mite is to flourish, and the disease may often be cured by no other treatment than the supply of nourishing food and generally healthy conditions, whereas in man condition, age, sex, temperament, etc., are entirely unimportant. Indeed really sick, feverish subjects with serious inflammations do not furnish a favourable ground for scabies, which soon dies out upon them. Typhoid patients heal spontaneously during their fever, but on convalescence the scabies resumes its progress.

In the life of the male *Sarcoptes* four stages are recognised, egg, larva, nymph and adult. In the case of the female there are two nymphal stages, the second nymphal stage being remarkable inasmuch as it is ripe for fertilisation by the male but has not yet developed the orifice (tocostome) by which the eggs are laid. This second nymphal stage is sometimes called the immature female (femelle pubère).

Description of SARCOPTES SCABIEI.

Adult female. Length 330–450μ; breadth 250–350μ. Body oval and testudiniform, being convex above and flattened below; of a translucent dirty white colour with the more highly chitinised portions brownish. The integument is finely striate over most of its surface, the striae being mostly oblique on the dorsal aspect, and transverse on the ventral surface.

There is no definite segmentation of the body, but it is nevertheless (in the living specimen) fairly clearly divided into two regions by a fold of the integument, the division being more distinct ventrally. These two regions are generally called the cephalothorax and abdomen, which is, unfortunately, an entire misuse of those terms as applied to other groups of Arachnida, as the posterior portion bears the last two pairs of legs. The terms notothorax and notogaster applied to these regions in their dorsal aspect are perhaps less objectionable. Mégnin (1895, p. 130) says that the body is divided into five incomplete segments by dorsal furrows, and Fürstenberg evidently is of the same opinion. The integument is furnished with an armature of cones, spines, scales and bristles which must be carefully studied since they are regarded as of great taxonomic importance.

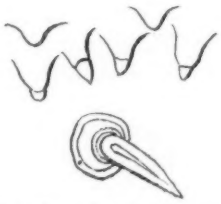
Dorsal aspect. The fine parallel striae are for the most part absent on a large median posterior space (the posterior part of the notothorax and the whole of the notogaster) which is beset by about 140 minute conical scales, roughly arranged in transverse rows, and with their points directed backwards. Fürstenberg has figured these scales under a very high magnification and considers their particular shape characteristic of this species. They are mostly of the acorn-shaped variety. (Text-figure 1.)

On the notothorax there is also a rectangular space free both from striae and scales but with a shagreened or rugose surface. This is the "clairière" of French and the "Blösse" of German writers, and it is the "plastron" or specially chitinised plate of Mégnin, who noted it first in the horse *Sarcoptes*, where its slightly yellow colour attracted his attention, but found it subse-

quently in all the varieties of *Sarcoptes* he was able to examine (*vide supra*). Munro (1919) figures, but does not mention, two small spots in front of the plastron which are probably Mégnin's "rudiments of stigmata." (Pl. XV, fig. 10.)

On either side of the notothorax, just posterior to this "plastron," there are three *notothoracic cones*, arranged in a triangle with its apex posterior. These "cones," which are in fact somewhat lancet-shaped, are articulated into the crater-like centre of circular low eminences.

On either side of the notogaster are seven backwardly directed spines, roughly arranged in two longitudinal rows, an inner row of four and an outer of three spines. These spines are of the same nature as the notothoracic cones, but more elongated. These spines, cones and scales are all calculated to render retrograde movement in its burrow impossible to the parasite.



Text-figure 1. Dorsal scales and a notogastric spine of *S. scabiei* (after Fürstenberg).

The chaetotaxy, or arrangement of bristles, is especially important and none of the figures of the early investigators are accurate in this respect. Munro (1919), who both studied the literature on the subject and examined much fresh material, gives it as follows:

On the notothorax there are four pairs of bristles:

(1) a pair "lying just below the camerostome." This appears to refer to the largest of three pairs of bristles which he figures as arising from the rostrum (see Pl. XV, fig. 10).

(2) a small pair close together near the anterior border.

(3) a pair of strong whip-like bristles, one on either side of the clairière or plastron, and reminiscent, as Munro says, of the pseudostigmatic organs of the Oribatidae. As a matter of fact it is quite common in various acarine groups (Gamasidae, Tyroglyphidae, etc.) to find strong bristles in this position, and it is possible that they have a special sensory significance—as they certainly have in the Oribatidae. When Fürstenberg, however, alludes to the "Tasthaar" he means the stronger of the two lateral hairs mentioned in (4).

(4) a pair of bristles (or hairs) on each side just anterior to the fold separating notothorax and notogaster, the anterior (and according to Munro's figure the more dorsally inserted) bristle being the longer. (This is Fürstenberg's Tasthaar.)

On the notogaster there is a pair of bristles on either side of the terminally situated genito-anal aperture, the inner bristle being somewhat longer than the outer.

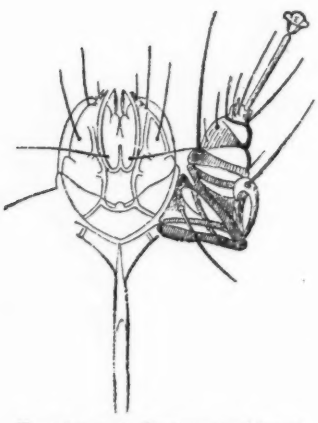
Ventral aspect. The rostrum and legs will presently be described in detail, but it is necessary here to mention the epimeres, which are striking features of the ventral surface, and have been considered of great taxonomic im-

portance. They are chitinous bars produced into the body from the skeletal tissues of the legs, and are arranged as follows:

From the first pair of legs the epimeres run inwards and meet just behind the base of the rostrum and are then produced backwards in a single sternal rod, ending in a fairly sharp point; the epimeres of the second legs are free and slightly curved, converging towards the sternal bar without reaching it, and ending at about the same level. Precisely how they terminate seems doubtful, whether in rounded knobs or in a slight fork. The epimeres of the third and fourth legs are short and curve towards one another till they nearly meet, but they do not fuse.

Immediately behind the end of the sternal bar is a transverse slit—the tocostome, or aperture for egg-laying, guarded by three very short bristles (see Pl. XV, fig. 11). There is also a pair of short bristles one on either side of the middle of the sternal bar, and another short pair between the fourth pair of legs.

The legs. The two anterior pairs of legs arise from the margin of the body and are larger than the third and fourth pairs, which arise from the under surface of the animal. Moreover the two first legs terminate in *ambulacra* (ventouses), long tubular processes ending in a bell-shaped sucker, while these ambulacra are not found on legs 3 and 4, each of which is produced into a long bristle. Each leg consists of five articles (coxa, trochanter, femur, tibia and tarsus according to Dubreuilh and Beille), and has a strong chitinous skeleton, each article being strengthened by a chitinous ring, and there being also, apparently, an obliquely placed ring of chitin connecting the rings of the first two articles (Text-figure 2). The anterior legs have three claws, one (discovered by Mégnin as described above) on the inferior side of the trochanter, and two, of unequal size, at the extremity of the tarsus near the origin of the ambulacrum. The ambulacrum itself is about as long as the whole limb. The legs are also furnished with a few bristles and some short spines (*piquants*).



Text-figure 2. Rostrum and leg of *Sarcoptes scabiei* (after Railliet).

The rostrum. The mouth-parts are enclosed in a sort of incomplete chamber, the *camerostome* formed by four prolongations of the integument—the epistome above, the cheeks (joues) on either side, and the hypostome (lèvre) below. They consist of six pieces, arranged in two rows; above are the chelicerae and pedipalpi, and below are the mâchoires (? labial palps) soldered to the sides of the hypostome and meeting posteriorly in a rounded plate, the mentum.

The pedipalps, which are above and slightly external to the "mâchoires" and just within the cheeks, are conical and three-jointed. Their chitinised base is contiguous to the epimeres of the first legs. The chelicerae are chelate and consist of a rod (tige) ending in two toothed processes, the inner of which is mobile. According to Dubreuilh and Beille (1895, p. 18) the dorsal edges of the chelicerae are in contact while their ventral edges are separated, so that there is between them and the hypostome a space, triangular in section, which is the mouth cavity. The chelicerae always act in alternation.

Delafond and Bourguignon (*Traité pratique*, p. 37) give a very interesting account of the mode of action of the mouth-parts. First the palps are separated and their sharp extremities plunged into the integument, which they loosen by repeated attacks. Then the chelicerae come into play, breaking down the adhesions "between the corneous and mucous layers," and acting alternately. Now the muscles which actuate them pass through a narrow orifice to the thorax, and this would result in pulling the left mandible to the right, and the right to the left. This is prevented by a small horny plate which separates the mandibles behind and turns on a fixed vertical axis.

ADULT MALE. The male differs from the female in the following respects. It is much smaller, measuring 200–235μ in length by 145–170μ in breadth, and the fourth pair of legs terminate, like the anterior legs, in ambulacra. The epimeres of the second pair of legs are forked at their extremity[1], and the epimeres of legs 3 and 4 are not only fused together at each side, but the two pairs of epimeres are united by a transverse bar from the middle of which a chitinous structure in the form of an inverted **Y** proceeds backwards and constitutes the *epiandrium* or genital armature, for the genital aperture of the male lies between the fourth pair of legs, while the anus, as in the female, is terminal.

The dorsal aspect presents three "plastrons" or "clairières," one on the notothorax and two on the notogaster. That on the notothorax is much larger than in the female, and is longer than broad. Those on the notogaster are small and subcircular and lie on either side of the posterior end of the abdomen.

The immature stages. There appears to be no detailed account of the structure of any of the immature stages of *S. scabiei*. Munro thus describes the second nymphal or immature female stage (femelle pubère).

"Length 220–250μ; breadth 170–200μ; rugose area (plastron) rectangular; dorsal scales numerous; bare area notogastric, small; notogastric spines twelve in number; third and fourth posterior legs ending in bristles; epimeres of anterior pairs of legs (? the second pair) forked. Tocostome and tocostomal hairs absent."

The first nymphal stage, according to Dubreuilh and Beille (p. 20) had

[1] Fürstenberg maintains that in this species the epimeres of the second legs do not end freely but are joined by a transverse bar of chitin just anterior to that connecting the epiandrium with the epimeres of the posterior legs (*Krätzmilben*, Pl. I, fig. 8).

never been observed in the human *Sarcoptes*, but Munro found it on two occasions, and describes it as follows:

"Length 160μ; rugose area indistinct; dorsal scales numerous, bare area well defined; notogastric spines twelve in number. Fourth pair of legs ending in bristles which are shorter than those of the third pair; only one pair of anal bristles present. Epimeres of the anterior pairs of legs forked."

Dubreuilh and Beille (p. 20) say that the nymphs are of two sizes (measurements not given) and that the smaller produce males and the larger females.

The larva is hexapod, the last pair of legs ending in bristles. Its length is from 110 to 140μ and its breadth 90 to 110μ. Rugose area ill defined; dorsal scales indistinct except at the sides so that a large bare area is present; notogastral spines ten; only one pair of anal bristles.

The characters which have generally been relied on to separate the various forms which have been regarded by some authors as distinct species and by others as varieties are size, shape, the rugose areas, the epimeres, and the number and particular pattern of the various spines, scales, etc., which go to make up the dorsal armature. It has to be noted that the limits of size in a single form like *S. scabiei* are very considerable, and that the shape is necessarily rather indefinite in animals so feebly chitinised, while the other characters are so minute and so difficult of observation that no two writers are absolutely in agreement in their description of any one variety. It would seem to be the first task of a new investigator to examine minutely the human sarcopt in its various stages and to determine authoritatively the details of its structure, verifying or rejecting the statements of previous writers. When this is once accomplished the ground will be cleared for a comparison between it and the forms which affect other mammalian groups.

Life-History of the Sarcoptes of Man.

Excavation of the gallery. Immediately after her last moult the female begins to burrow, showing a distinct preference for certain regions. If confined under a watchglass she may be caused to burrow anywhere, but only sufficiently to bury herself. If free to wander, she selects either the interdigital spaces, the wrists and their ulnar margin, the elbows, the anterior folds of the axillae, the pubic area, the buttocks, the back of the knee, the ankle or the toes.

Holding on by the suckers of the anterior legs she raises the hind end of the body on the bristles of the posterior legs till her position is almost perpendicular, and commences to cut into the skin. She can completely bury herself in 2½ minutes (Munro, p. 15). When concealed, she may either remain inert for a time or continue burrowing, and this depends somewhat on the temperature, which, according to Delafond and Bourguignon, must be between 10° and 30° C. Normally the burrowing only occurs at night, when the patient is warm in bed, but it may be induced by artificially warming the place where the parasite has buried itself. Munro (p. 15) found that the average length of

burrow daily excavated was between two and three millimeters. Török and Dubreuilh have shown that the galleries are entirely confined to the corneous layer.

A fairly constant characteristic of *Sarcoptes* burrows is the presence of vesicles (vésicues perlés), minute translucent indurated swellings, which are regarded as second only to the galleries themselves in diagnosing scabies. It was these vesicles which misled investigators at the beginning of the 19th century, for they sought in vain for the mite in their interior—though Moffett had stated as early as 1634 that it was not to be found in them, but in their neighbourhood. The vesicle, indeed, forms *below* the gallery, a short distance behind the burrowing mite. The gallery and the vesicles seem to be directly attributable to the *Sarcoptes*, but the other complications which so frequently attend severe scabies must be regarded as secondary.

Oviposition. The mite deposits eggs in groups of 2–4 (Gerlach says 3–6) as she proceeds with her burrowing, resting after each act of deposition. Black masses of excrement are found in the neighbourhood of the eggs. The eggs are oval, $150 \times 100\mu$. They appear to be laid in a varying condition of development, which may partly account for the very varying incubation periods allowed by different writers. Bourguignon gives ten days and Fürstenberg seven days, but Gerlach states that this is certainly inaccurate, and that the usual period is 64–76 hours. Munro agrees with the latter estimate when nothing has happened to delay matters, but he says that partially developed eggs may have their development arrested by unfavourable conditions and afterwards resume it.

Unless disturbed the female makes a single burrow and dies at the end of it. The burrow is always sinuous, and just the width of the mite. It may attain 3 cm. in length. At intervals there are holes in the roof—to admit air or for the egress of the larvae and nymphs. The number of eggs is doubtful—possibly because few burrows are entirely undisturbed. The largest number actually found in a burrow seems to be 21, but there exists a pretty general belief that the female lays in all about 40 or 50 eggs.

The larvae. Several authors (Hebra, Railliet, Dubreuilh) state that the larva moults three or four times. Munro found no evidence of this. They live in the burrows and bore into its floor, or emerge and burrow deeply into the skin outside—more deeply, according to Gerlach, than the females themselves.

The nymphs. Nothing has been observed as to the habits of the first-stage nymph. The second-stage nymph (femelle pubère) makes a burrow like that of the adult but smaller, and devoid of vesicles. These short burrows have lateral branches or pockets excavated by the male (Munro, p. 22).

Mégnin (1893, p. 132) says that he has found the human *Sarcoptes* on small house-dogs, and very frequently on ferrets, and that Railliet has found it on rabbits.

The above is a condensed account of the structure and life-history of the human *Sarcoptes* as at present known, and it is now proposed to deal briefly with the forms which are generally considered distinct from it. In order not to prejudge their status it will be as well to allude to them simply under the names of the animals they affect, leaving open the question as to whether they are species, varieties, or merely races. The characters which are supposed to distinguish them from the human *Sarcoptes* will be indicated, and anything else of importance to our purpose will be added.

A good plan will be to give the *Tierreich* definition of each form at the outset. It aims at the briefest possible characterisation, and provides a convenient starting point.

Many of these forms have been naturally and artificially communicated to different animals from their proper hosts, and the matter will be referred to in due place, but in this connection Delafond and Bourguignon utter a warning which is very much to the point. Artificial attempts to communicate scabies from one animal to another frequently fail, but too much importance must not be attributed to such failure. Probably in nature there are many abortive attempts at invasion of another animal before success is attained, and in artificial infection the conditions are generally much less favourable. Comparatively few mites are transferred, and many of these may be unsuited, from their nature (*e.g.* unfertilised nymphs) or from their condition through injury in the act of transference, to establish the disease on an animal which might very well succumb to repeated natural invasions.

SARCOPTINAE PARASITIC ON OTHER ANIMALS.

Scabiei-crustosae.

Tierreich: Fürstenberg, 1861.

Dorsal scales blunt; no rugose area; notogastric spines long and pointed. The epiandrium reaches the epimere.

♀ 410 × 340μ.

♂ 170 × 150μ.

Man; causing Norwegian itch. Norway, Germany, France.

Fürstenberg's description is in substance as follows:

Female. Body nearly round, not much longer than broad, the fourth thoracic segment prominent at the sides, the sensory hair borne on it being very long[1]. Back with scale-like prominences surrounded by a rim of chitin. Six long notothoracic cones and 14 curved, very sharp notogastric spines.

Male. Body nearly round; fourth thoracic segment rather prominent, with strong, long sensory hair. Very few dorsal scales, at the edge of the thorax and abdomen. A shield-like area (Abgrenzung) finely punctate and

[1] This is the third dorsal hair, the more anterior of Munro's two lateral hairs. Fürstenberg believed that folds—often conspicuous at the sides—indicated primitive segmentation.

rounded behind, extending from the head to the fourth thoracic ring. Epiandrium firmly fused with epimere.

This *Sarcoptes* is the cause of "Norwegian itch" in man, and lives in innumerable superimposed burrows in the crusts. Chaetotaxy like that of the common human *Sarcoptes*, but the folds of the body are more marked. ♀ 415 × 341μ. The head is comparatively large.

The male is rather smaller than that of the common human *Sarcoptes*—172 × 153μ. (Fürstenberg, p. 212, Pl. V.)

Text-figure 3. Examples of dorsal scales of *S. scabiei-crustosae* (after Fürstenberg).

The disease of "Norwegian itch" was (according to Railliet) first recorded by Boeck and Danielssen in 1848. It is characterised by gigantic crusts. Sometimes these arise at the outset, but more often they do not appear for several years (3–9). Callosities 1–6 mm. in thickness appear on the palms of the hands, the soles of the feet, the wrists, elbows and knees. The scabies may extend to the face and the hairy scalp.

Mégnin thinks this parasite identical with *lupi*, but Railliet considers them too unlike.

Fürstenberg considered the peculiar severity of the disease due to the particular *Sarcoptes* at work, but Hebra attributes it to special susceptibility of certain subjects, and considers the parasite to be nothing but the common human *Sarcoptes*. It has been noted not only in Norway, but in France, Austria, Germany, Denmark, Russia and Turkey.

Lupi.

Tierreich: Mégnin, 1880.

Dorsal scales pointed; no rugose area; notothoracic cones long and blunt. ♂ very elongate (langgestreckt). Epiandrium firmly united to epimere.

♀ 370–400μ × 280–300μ.

♂ 270 × 160μ.

Canis lupis. France.

Mégnin's measurements are:

♀ 400 × 280μ. ♂ 270 × 210μ.

He found it in 1875 in four young wolves (at the Muséum de Paris) which had their hides covered with thick, yellowish, moist crusts, nearly a centimeter thick in places. Transferred to a horse, they gave rise to a scabies of exactly the same nature—even to the characteristic smell. Mégnin considered it the cause of "Norwegian itch" (*vide ante*) but his view is not universally accepted.

Equi.

Tierreich: Gerlach, 1857 (von Hering, 1838).

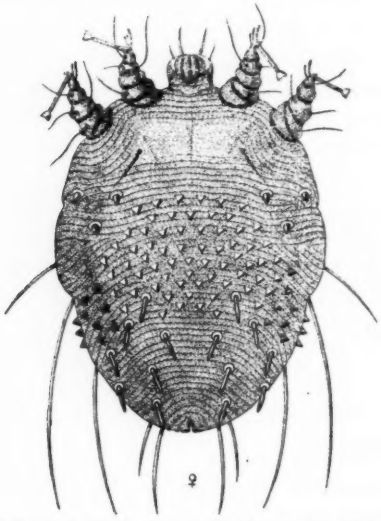
Dorsal scales small, scarcely longer than broad; an anterior and a posterior rugose area; notogastral spines blunt; notothoracic cones very short; epiandrium scarcely reaches the epimere.

♀ 450–500μ × 310–370μ.

♂ 230–280μ × 150–200μ.

Horse, but can flourish on ass, mule and man for a short time.

This form was independently discovered by Gerlach and Delafond simultaneously. It is the cause of "dry mange," "symptomatic mange," or "epizoötic mange" in the Equidae (Gerlach, 1857, p. 116, Pl. II, figs. 8–10).



Text-figure 4. *Sarcoptes equi*, ♀, according to Railliet.

Gerlach says the ♀ is somewhat longer and narrower than the human *Sarcoptes*, but is only to be distinguished when seen in the bulk; his measurements of the ♀ (reduced from fractions of an inch to microns) are 440 × 300μ.

Delafond and Bourguignon remark that the "solipèdes" have two mange parasites, a *Sarcoptes* and a *Psoroptes*, the former transmissible to man, the latter not. (There is also a Chorioptic scabies of the horse.)

Neumann (p. 131) says "Sarcoptic scabies begins most frequently at the withers, and extends to the sides of the neck, shoulders, back and sides. It does not easily invade the extremity of the limbs, and it respects the parts covered with strong hairs. The Psoropt, on the contrary, appears to seek the parts avoided by the Sarcopt."

There is first pruritus, then depilation, then formation of crusts. Many experiments have been made on the transmission of *Sarcoptes* from other animals to the horse, and of the horse *Sarcoptes* to other animals. Delafond and Bourguignon several times succeeded in transferring the human Sarcopt to the horse, where it burrowed galleries, but always died out after a short time. They also describe a case in which horses groomed with brushes and sponges which had been used to clean mangy lions contracted the disease—which was artificially cured. According to Neumann (p. 133) Wallraff reports a case of horses contracting scabies from mangy goats.

There are many cases of the transference of the horse Sarcopt to man (*e.g.* Delafond and Bourguignon, *Traité pratique*, p. 295). It usually disappears spontaneously in from 15 days to 6 weeks, or at all events easily yields to treatment.

Mégnin (1893, p. 144), in May 1892, investigated an extraordinary case of very severe crusted scabies in man and found the sarcopt to be that of the horse. The patient had had charge of a horse hauling barges on the Oise.

Neumann (p. 134) says "Sarcoptic scabies of the horse appears to be capable of transmission to the bovine species, though up to the present time no one in practice has observed this form of mange in cattle. The possibility of this transmission rests on facts published by Robert Fauvet and Grognier."

The following results of experiments by Delafond and Bourguignon on the longevity of the mite may be given here.

(1) 10 ♂, 10 larvae and 10 ♀ in a glass tube covered with paper, in a room at temp. 10°–15° C.

larvae died from 4th to 6th day,
males „ „ 5th to 8th „
females „ „ 6th to 9th „

(2) Experiment repeated in a stable at temp. 15°–20° C.

larvae died from 5th to 6th day,
males „ „ 6th to 8th „
females „ „ 9th to 10th „

(3) When kept in tubes containing hairs and fragments of crust and litter, and moistened from time to time (at 15°–20° C.)

larvae lived 10 days,
males „ 13–14 days,
females „ 14–16 „

Gerlach kept the mites alive three or four weeks in a piece of mangy skin kept moist.

Hering's *S. equi* was the *Psoroptes* of the horse.

Canis.

Tierreich: Gerlach, 1857 = *squamiferus* Fürst. (in part).

Dorsal scales hardly longer than broad; no rugose area; notogastral spines long and slender; anterior arm of epiandrium feebly connected with epimeres of legs 3 *and* 4.

♀ 300–450μ × 230–350μ.

♂ 190–250μ × 160–180μ.

Dog, appears to be communicable to man but not to other animals.

There is great confusion with regard to the dog *Sarcoptes*. This animal is, of course, subject to a Demodicic mange, but several authors record a Sarcoptic scabies of the dog, though no two writers agree about it.

Gerlach's *canis* is "smaller than the human species with legs of a darker yellow-brown colour," but he describes and figures (Pl. II, fig. 11) the ♀ with two posterior rounded projections though the male has no corresponding "cylinders." His measurements of the ♀ are 300 × 225μ. Now he described at the same time a form from the pig which he called *suis*, the female of which had no such projections, but the male of which is described and figured with two "cylinders" near the generative opening (Pl. III, fig. 16). Fürstenberg (1861) considered these two forms the same, and fuses them under the name *squamiferus*, but he omits the projections on the abdomen of Gerlach's ♀ *canis* and the "cylinders" of Gerlach's ♂ *suis* (Fürstenberg, p. 214, Pls. II and IV). Delafond and Bourguignon (1862) threw doubt on Gerlach's *canis* because of the abdominal projections, which, they alleged, would remove it from the genus *Sarcoptes* altogether, but they knew of a dog *Sarcoptes* which Bourguignon had described in 1853 (thesis for a prix de Montyon), which was "notably smaller than the human *Sarcoptes* (♀ 300 × 250μ, ♂ 200 × 160μ) but had the same form."

Text-figure 5. Dorsal scales and a notogastral spine of *S. canis* (*squamiferus*) (after Fürstenberg).

On the other hand Canestrini (*Prosp. Acarofauna Italiana*, VI. p. 741, Pl. 63) describes and figures the Sarcopt from a Neapolitan dog, the female measuring 450 × 350μ.

Delafond and Bourguignon (1862) performed many experiments with the *Sarcoptes* they found on the dog. Healthy dogs confined with mangy dogs caught the disease. Crusts placed on unhealthy dogs communicated it in a severe form. A dog powdered with the mites from the skin of another dog which had died of mange and then badly fed and housed, contracted scabies which was allowed to go to extreme lengths, but there was spontaneous cure on the resumption of good feeding and housing. This experiment was repeated.

Conditions of age and race are important. Long-haired dogs favour sarcoptic mange, as do masterless or ill-tended dogs and chained dogs with damp kennels. Good housing is of the utmost importance.

Sarcoptic mange of the dog is alleged by different writers to be not uncommon, but investigators have generally had a difficulty in finding it. It usually begins on the head, muzzle, round the eyes and on the ears, but may appear on any part of the body (*Traité pratique*, p. 184 *et seq.*).

In any new investigation this form must be considered in connection with that obtained from the pig which is next discussed.

According to Neumann (1905, p. 183) the dog is also subject to the form *lupi*.

Besides a Demodicic mange, and scabies due to the *Sarcoptes* above mentioned, a Chorioptic mange may be found on the dog.

Suis.

Tierreich: Gerlach, 1857 (*squamiferus* Fürst. in part).

Dorsal scales longer than broad, pointed; an anterior rugose area; motogastral spines long, slender, pointed; epimere of legs strongly curved outward; epiandrium reaches the epimere; body nearly globular.

♀ 350–500μ × 290–390μ.

♂ 250–350μ × 190–300μ.

Sus domesticus. Transmissible to man. Germany, France, Italy.

Gerlach (1857) says that Gurlt had found it many years previously on wild boars, and since then Hertwig and Gerlach had recorded it from wild swine. Gerlach's measurements of the ♀ (reduced from fractions of an inch to microns) are 380 × 270μ (Mégnin gives the measurements ♀ 500 × 360μ, ♂ 320 × 290μ, and Neumann gives ♀ 400–500μ × 320–390μ, ♂ 250–350μ × 190–300μ). Gerlach describes it as very like that of man, and that of the horse, between the two in size, and conspicuously broader in front and narrower behind, even discounting the fact that the abdominal width varies according to the contained eggs. He, however, gives the ♂ two genital "cylinders" (Gerlach, Pl. III, fig. 16).

Delafond, in 1857, found on the domestic pig a *Sarcoptes* which he considered identical with that of man, but Mégnin, who has examined Delafond's microscopic preparations of it, says it is Gerlach's *suis* (Mégnin, *Ac. parasites*, p. 140). Fürstenberg considers Gerlach's *suis* and *canis* identical, and redescribes them as *squamiferus* (see *canis*).

Mégnin thought the pig had two *Sarcoptes*—a large form on the body and a small form in the ears. The latter, whose existence has been disputed, is next dealt with under Canestrini's name *parvulus*. The ordinary pig sarcopt first occurs on the head—chiefly the ears and round the eyes; then the withers croup, and inner surface of the thighs. Later, the whole body. No galleries are observed, but when advanced there is abundance of crusts.

It is transmissible to man and to the dog, but soon dies out. This is the largest known *Sarcoptes*.

Parvulus.

Tierreich: Canestrini, 1894.

Body (Rumpf) very small.

♀ 288 × 216μ.

♂ 168 × 128μ.

In outer ear passage of Sus domesticus.

This species (or variety) is merely nominal, the name having been given in 1894 by Canestrini to a very small form found by Guzzoni in 1877 in the ears of a pig. Gurlt and Spinola, Gerlach, Mégnin and Railliet (1895, p. 635) appear to have come across the same form, but there is no description of it. Neumann (1905, p. 177) states definitely that there is no reason to believe in the existence of a second pig sarcopt, but he does not explain the great difference in size between the particularly large form usual on the pig and the minute form alleged by several observers to occur in the ears of that animal.

Furonis.

Tierreich: Railliet, 1893.

Dorsal scales dense (dicht), slender (fein); an anterior rugose area; epiandrium firmly united to epimere.

♀ 330–420μ × 270–300μ.

♂ 210–220μ × 160–180μ.

Mustela furo. France.

The measurements are those given by Railliet (1895, p. 656), who says the *Sarcoptes* was first described by Peuch in 1869, and that it is very common on the ferret, which probably contracts it from rabbit burrows frequented by polecats. It principally attacks the head and legs, but sometimes invades all the surface, causing brown or yellowish crusts. On the feet, the crusts especially occur on the plantar surface and at the base of the claws, which often become abnormally long and turned upwards. Peuch, though he made many attempts, did not succeed in transmitting it either to man or to the dog.

Peuch's account was published in 1869 and this I have been unable to consult, but it seems to be chiefly clinical, and the meagre details obtainable are those furnished by Railliet (1895, p. 656). He calls the dorsal scales *minces et serrées*, and says that the rugose area is faint.

Cuniculi.

Tierreich: Neumann, 1892 (*Rev. Vét.*, March, 1893).

Dorsal scales numerous, sharp, as long as broad; no rugose area; notogastric spines broad at the base, bluntly pointed; epimere of leg 2 of ♀ strongly bent outwards; front arm of epiandrium rudimentary, not reaching the epimere.

♀ 410–440μ × 320–340μ.

♂ 230–250μ × 170–180μ.

Lepus cuniculus. France, Italy.

Neumann's paper has been unobtainable, and he does not describe this *Sarcoptes* in his *Parasites*. Railliet (1895, p. 656) says: the dorsal scales of the ♀ are not very sharp but rather strongly chitinised, at least in front and at the sides. A posterior "clairière." Epiandrium rather loosely connected with epimere. ♀ 340–400μ × 260–300μ, ♂ 210–228μ × 155–178μ. Oviparous or viviparous.

Its habits seem to be precisely like those of *furonis* in the ferret. It affects in turn the nose, lips, chin, the base of the claws, and the plantar surface of the feet, sometimes extending to other parts, and causing greyish crusts. The disease is very contagious among rabbits and often ends fatally in a few weeks. Neumann did not succeed in communicating it to dog, sheep, ox, pig or horse, but Railliet succeeded in the case of the capybara and the ferret.

The question naturally arises as to whether this form is distinct from *furonis*. The chief differences seem to be its larger size, and the connection between the epiandrium and the epimeres of legs 3 and 4. The rugose area might well escape observation.

Canestrini calls this form *S. praecox*, considering *cuniculi* preoccupied for *Notoedres* (*vide infra*). He gives (*Prosp. Acarof. It.*, VI. Pl. 69) a figure of the ♂ showing the trochantal claws on leg 1—alleged by Mégnin to be always present in *Sarcoptes*.

Ovis.

Tierreich: Mégnin, 1880.

Dorsal scales not numerous; an anterior and a posterior rugose area (*or clear space*) *not very extensive* (*ausgedehnt*). *Epiandrium feebly connected with epimere.*

♀ 314 × 300μ.

♂ 220 × 160μ.

Ovis aries. France, Italy.

Delafond (1858) was the first to find this parasite, which, of course, must not be confounded with the cause of "sheep scab" (which is a *Psoroptes*), or with the *Chorioptes* which also affects this animal. It causes "black muzzle" or "face mange," and is much less common than the *Psoroptes*.

It only attacks parts free from wool, first appearing on the upper lip and round the nostrils, and later invading the face, forehead, cheeks and eyelids, and sometimes the intermaxillary space. When of long standing it may appear between the fore-legs, on the belly, and round the joints.

Delafond's subjects were Neapolitan sheep brought to Paris. Both the *Psoroptes* and the *Sarcoptes* were present, and a pupil (Polvent) at the Alfort Veterinary College who treated them became badly infected by the *Sarcoptes*, which Delafond considered to be exactly like that of man. The pupil, though in a terrible condition, persisted for 49 days without treatment, but was then so ill that cure was undertaken. This occupied a fortnight.

The *Tierreich* measurements are those given by Mégnin.

Vulpis.

Tierreich: Fürstenberg, 1861.

No rugose area; notogastral spines long and pointed; notothoracic cones longer than usual; anterior arm of epiandrium well developed.

♀ 442 × 315μ. ♂ 245 × 185μ.

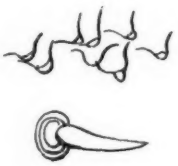
Canis vulpes.

Fürstenberg's description is in effect as follows:

Female. Body long-oval, testudiniform; dorsal scales in rows; notothoracic cones rather long, curved, with the points bent backwards and downwards. Notogastric spines long, not very strong, slightly curved, and apparently sharp-pointed. 442 × 315μ.

Male. Body nearly round, not much longer than broad; a few dorsal scales, only at the boundaries of the thorax and abdomen; otherwise with the armature of the ♂ of *Scabiei-crustosae.* 245 × 185μ.

Text-figure 6. Notothoracic cone, dorsal scales, and notogastric spine of *S. vulpis* (after Fürstenberg).



Text-figure 7. Dorsal scales and a notogastral spine of *S. caprae* (after Fürstenberg).

The female, though inferior to the human *Sarcoptes* in size, resembles it in general appearance. The bulging of the fourth thoracic segment is not so marked as in *Scabiei-crustosae*, and the sensory hair is only of medium size.

The disease it conveys is like that of *Scabiei-crustosae*, causing crusts often half-an-inch thick.

The specimens were from a mangy fox, the tail of which was sent to Fürstenberg by his brother in 1857 from Gagen in Rügen. It arrived three days after the animal was killed, but the mites were still alive, and continued to live three or four days more (Fürstenberg, p. 213, Pl. VI).

Railliet (1895, p. 659) says that Walz first recorded this mite in 1809.

Caprae.

Tierreich: Fürstenberg, 1861.

Dorsal scales blunt (stumpf); a posterior faint rugose area; epiandrium feebly connected with epimere.

♀ 345 × 342μ. ♂ 243 × 188μ.

Goat, sheep, horse, ox and man.

The main points of Fürstenberg's description are these:

Female. Body nearly round, the thorax broader than the abdomen, the folds at the side moderately deep. Dorsal scales short, ending in a terminal chitinous portion which is generally rounded, sometimes pointed—only occasionally nail-like (genagelte) scales. Notothoracic cones long, acorn shaped; notogastric spines fairly long and apparently sharp-pointed. $345 \times 342\mu$.

Male. Oval, nearly egg-shaped, a few marginal dorsal scales. $243 \times 188\mu$.

They live in the skin and crusts of Egyptian pygmy goats (Zwergziege). The specimens were sent by Prof. Müller of Vienna (Fürstenberg, p. 214, Pl. VII, figs. 72–79).

The disease chiefly affects the head and ears, then the trunk, and lastly the limbs. It is often epizoötic with considerable mortality. Wallraff recorded a case in Grisons during the years 1851–4. In the spring of 1853, out of 2596 goats 1015 had developed mange and 250 had died. At the end of the attack 500 goats had been lost.

Henderson recorded it in 1851 from a Persian goat in London. Except for the Swiss cases it has always been found in African or Asian varieties of goat.

It seems readily transmissible to other animals, and in the Swiss epizoötic horses, oxen, sheep, pigs and especially man caught the disease from the goats, and had it in a severe form. In Henderson's case it passed to the horse and thence to man.

Delafond and Bourguignon (1857) say: "this species is remarkable for the size of its ambulacra (ventouses) on the anterior legs, and for the length of its posterior hairs."

Hebra found no difference between this *Sarcoptes* and that of man.

The goat is also subject to a Chorioptic scabies.

Leonis.

Tierreich: Canestrini (the "Sarcopte du lion," Delafond and Bourguignon, 1862).

Dorsal scales longer than broad; notogastral spines long, slender, pointed; notothoracic cones short, blunt, swelling in the middle; epiandrium feebly united to epimere.

♀ $460 \times 350\mu$.

♂ $250 \times 180\mu$.

Felis leo. Ménagerie Pianet, France.

Canestrini (*Prosp. Acarof. It.*, VI. Pl. 64) figures this sarcopt from preparations sent him by Trouessart. They were prepared by Neumann, and bore the label "*Sarcoptes scabiei* du lion, Ménagerie Pianet, 3, v. 92." The ♀ shows remarkable dorsal projections of the armature of the first legs.

The long account given by Delafond and Bourguignon (1862, pp. 229–233) remains our chief source of information about this *Sarcoptes*—which, however,

was considered by those authors identical with that of man. Borelli brought to Paris in his menagerie five terribly mangy lions, from which five assistants contracted severe scabies. Less severely, six horses and three grooms were affected, and in addition a bear and a hyaena, after holding out as long as their general health was good, lost condition and then quickly succumbed.

Delafond and Bourguignon attempted to transmit the disease to rabbits and guinea-pigs, without much success. They conclude that this form of scabies is particularly severe, nearly always proving fatal in a short time, but that it requires a predisposition on the part of the animal attacked.

Dromedarii.

Tierreich: Gervais, 1841 (*Ann. Sci. Nat.*, Ser. 2, xv. p. 9).

Dorsal scales longer than broad, sharp-pointed, numerous; no rugose area; notogastral spines long, narrow, rather blunt at the end; notothoracic cones, twice as long as they are broad at the base. The epiandrium is not connected with the epimere.

♀ 360 × 330μ.

♂ 290 × 180μ.

Camel, llama, giraffe, Antilope bubalis—not man.

Canestrini (*Prosp. Acarof. It.*, vi. Pl. 62) figures the ♂ and the larva of this form. The trochantal claws appear to be very conspicuous.

Gervais obtained his material from a mangy dromedary brought from Africa to the Jardin du Roi, and killed as soon as its condition was recognised. He deals in the paper cited with the *Psoroptes* of the horse, the *Sarcoptes* of man and the present form, and gives figures. He says the two *Sarcoptes* so closely resemble each other as to be easily confused without close examination. "One might even suppose that it is to this similarity of organisation that it owes the power of passing with such facility from the animal to which it is proper to man, and of transmitting the disease from one to the other."

It appears, therefore, that the *Tierreich* account is wrong as regards man.

Gervais proceeds: "The form is almost the same, but the *Sarcoptes* of the dromedary is a little more elongate than that of man; the papilliform tubercles of the back have not quite the same disposition; in the human species the bilateral hair is larger and more recurved, and the inner pair of posterior hairs are the longer" (whereas in *Dromedarii* they are the shorter).

He adds some obscure statements about the epimeres, and says that the dromedary *Sarcoptes* is larger, "which no doubt accounts for the more intolerable pain it inflicts when it attacks man."

The four "doubtful species" of the *Tierreich* are little more than names, taken from the animals on which the scabies was observed, and they may be rapidly dealt with. They are *aucheniae, hydrochaeri, rupicaprae* and *wombati*.

Aucheniae.

One among a number of llamas, sent to France in 1858 and deposited at the Muséum de Paris, became mangy and was sent to the school at Alfort, where Delafond and Bourguignon examined it. The following year there were four more cases. The *Sarcoptes* gives rise to a scabies which becomes very rapidly generalised and forms large greyish crusts, very hard and adherent. The disease was contracted by two pupils who handled the animals, and they were so severely attacked that treatment was necessary after a month. Delafond and Bourguignon (1862, p. 383) say that the parasite is "like that of man, the dog and the lion," but add that "the male has, as special character, a short, slender, sharp appendage on the outer side of the ambulacrum."

Railliet (p. 634) says that the dorsal scales leave no "clairière," and that the measurements are ♀ 340 × 264μ, ♂ 245 × 182μ.

Hydrochaeri.

Found on *Hydrochaerus capybara*, the Capybara, Cabiai, or Carpincho of S. America and the W. Indies—the largest living rodent.

Mégnin (1893, p. 132) gives its measurements as ♀ 357 × 300μ, ♂ 220 × 160μ.

Neumann (1905, p. 190) says it attacks ferrets, and he apparently thinks it identical with *furonis*.

Rupicaprae.

According to Fürstenberg (p. 67), Hering (p. 603) says this *Sarcoptes* is roundish, narrowed posteriorly, irregular (höckerig) at the side, almost hairless, but the description is confused. Delafond and Bourguignon, judging from Hering's description and figures (which I have not seen), say that it is notoedric.

There is further confusion by Hering's statement that the female has two roundish projections, and the male a pair of suckers—which would remove it from the Sarcoptinae altogether.

Wombati.

There seems to be no description of this form. Duméril found it in the skin, covered with crusts, of a mangy wombat brought from Australia to the Muséum de Paris, and Fournier pronounced it to be identical with that of man. The keeper, and his assistants who prepared the skin, contracted an intense scabies with vesicles larger than those of the common scabies of man.

SARCOPTES ON CATTLE.

Robin in 1860 announced the discovery of a sarcopt on the ox, but the existence of a form proper to the bovidae has until recently been questioned and none has been described under the title *bovis*. Most of the old records of scabies in cattle were cases attributable to contagion with mangy animals

of other species—horses, cats or goats. Cases are, however, quite frequent, at all events in the British Isles, of a sarcoptic disease in cattle where no such origin can be traced, and until further investigation it must be held that a form of *Sarcoptes* exists with quite as sound a claim to the specific or varietal name *bovis* as have the other forms found on domestic animals to their respective titles.

Though the ox *Sarcoptes* has not been described and named, its occurrence has been frequently noted within the last 20 years, and there are at least two figures of it. M'Fadyean (1900, p. 73) gives an illustration of it which he states (in a footnote, *Ibid.*, XIII. p. 79) is a microphotograph, showing that it is an obvious *Sarcoptes*, and apparently proving that it possesses the unusual characteristic of three pairs of anal hairs. The second figure, also a microphotograph, is given by Williams (1917, p. 77), but the anal hairs are not distinct. I find, indeed, that the existence of a bovine sarcopt is no longer considered doubtful by veterinary surgeons, and that some economic entomologists are acquainted with it. It seems to be quite common in the north of England and in Scotland, and my friend Dr Stewart McDougal goes so far as to say that if he requires *Sarcoptes* for teaching purposes he finds cattle the most convenient source of material. It is clear that any investigation undertaken to determine the affinities between the sarcopt of man and those of domesticated and wild animals cannot afford to neglect the hitherto undescribed form which affects cattle.

Among the scattered and fragmentary records which possibly concern this sarcopt may be mentioned that of Bieler (1892) of Lausanne. He contracted a very severe form of scabies through carrying in his pocket, wrapped in paper, some hairs taken from a mangy bison.

Notoedres Railliet 1893.

The *Tierreich* definition is:

Male without anal cylinders, ♀ without copulation tubes. Long unjointed ambulacra on the two anterior legs of ♀ and on the two anterior legs and the second posterior leg of the ♂. Anus dorsal.

Oviparous parasites of mammalia.

Mégnin (1893, p. 145) says that *N. minor* differs from *S. scabiei* by smaller size, rounder body not showing any folds or constrictions, dorsal anus, and concentric undulating ridges in place of dorsal scales.

There appear to be two species of the genus (or subgenus) *Notoedres*, *minor* and *alepis*, of which the first presents two varieties.

N. minor Fürstenberg, 1861 (Syn. *S. cati* Hering 1838, *catorum* Küchenmeister 1855, *cati* and *cuniculi* Gerlach 1857, *Sarcopte notoèdre* Delafond and Bourguignon 1862, *S. notoedres* Mégnin 1876, *felis* Gerlach 1877). The scales are represented by concentric undulating lines round the dorsal anus. There are four slender spines on either side of the notothorax and six stronger

but still slender spines on either side of the anus. Ambulacrum with peduncle relatively short and terminal sucker large (Railliet). Two hairs longer than the rostrum on the epistome; a single pair of short anal bristles (Neumann).

1. Var. *cati*.

♀ 245–280μ × 165–175μ.

♂ 145–150μ × 120–125μ.

The cat scabies mite was seen by Gohier in 1813 but it was Hering (1838) who first attempted to describe it. He apparently found the male, which he considered the smallest Arachnid known. Fürstenberg fused *cati* and *cuniculi*, but Gerlach thought them distinct, and Mégnin and Railliet take the same view, though the differences are practically only physiological.

The scabies begins on the head and ears of the cat, but later invades the whole body. Though easily cured in its early stages it causes death, if untreated, in 4–6 months. A great many cases prove that it is easily communicable to man, but soon dies out spontaneously. Gerlach experimented on pupils at Berlin and on himself, but the disease always died out in from 10 to 20 days. All the clinical cases of cat scabies on man have been traced to contact with pet cats in a mangy condition.

Horses have acquired it from mangy cats reposing on their backs, and the same is said of the ox, though this is questioned. Gerlach attempted, unsuccessfully, to transmit it to the pig. Delafond and Bourguignon gave it to the dog—puppies dying of the disease. Mégnin places here the sarcopt found by Colin on the Coati, but Railliet thinks it was *N. alepis*.

2. Var. *cuniculi* (*S. cuniculi* Gerlach, 1857). This must be the "variété gliricole" of Mégnin (1893, p. 145).

♀ 215–235μ × 165–175μ.

♂ 142–155μ × 116–125μ.

Beyond the trifling difference of measurements there seems to be no visible distinction between *cati* and *cuniculi*, but their behaviour is not the same. It is severe on the rabbit, beginning at the muzzle and then invading the whole body, frequently fatal, because the animal is unable to feed. According to Mégnin (p. 145) it also affects the rat. Railliet found it only very slightly contagious. He could not transmit it to the rabbit by depositing crusts from a mangy rabbit on the shaved skin of a healthy subject, nor by cohabitation for 11 days. He did not succeed in communicating it to the dog, the cat or the rat.

N. alepis Railliet and Lucet, 1893.

Striations regular and concentric; no dorsal scales; four very slender spines on either side of the notothorax, and six on either side of the anus, which is more posterior than in *N. minor* (Text-fig. 8).

♀ 300–450μ × 230–400μ.

♂ 170–180μ × 130–140μ.

Legros observed this parasite on rats at the Jardin des Plantes in 1865, and Railliet and Lucet (1893, p. 404) found it again on "white mice," the black rat and the water vole. The disease is localised on the ears and the genitals, and apparently is never serious.

Railliet attributes Colin's Coati sarcopt to this species.

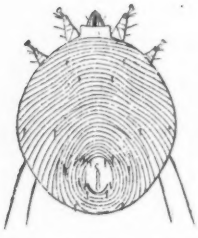
Cnemidocoptes Fürstenberg 1870.

The *Tierreich* definition is:

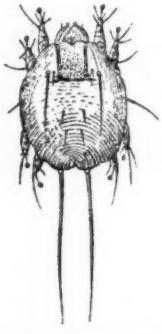
Male without anal cylinders; ♀ without copulation tubes; the mature ♀ without ambulacra; ♂ with long unjointed ambulacra on all legs; anus terminal.

Oviparous[1] (?) *parasites on birds.*

It is not proposed to deal in detail with this genus. It is entirely parasitic on birds, and its investigation would entail a quite separate branch of research.



Text-figure 8. *Notoedres alepis*, ♀ × 75 (after Railliet).



Text-figure 9. *Cnemidocoptes mutans*, ♂ × 100 (after Neumann).

Cnemidocoptes agrees with *Sarcoptes* and *Notoedres* in the nature of its mouth-parts and in its burrowing habits, and the type species *mutans* Robin, 1859 has long been known as causing scales and crusts on the domestic and game birds, and also on small birds in aviaries. Other species, however, have habits less akin to the usual sarcoptic method of life, and burrow into the feather-bulbs, causing deplumation. It will be sufficient to allude very briefly to the different forms which have been described. The general view seems to be that there are two species, *mutans* and *laevis*, with several varieties of the latter.

C. mutans Robin and Lanquetin, 1859.

Railliet (1895, p. 663) describes it thus:

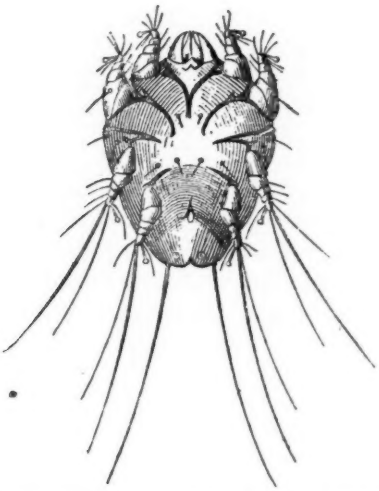
Rostrum broad, half concealed by epistome; ♂ 190–200μ × 120–130μ, body oval; no cheeks; conical legs, all with ambulacra; genital armature between legs 4.

[1] Fürstenberg calls *C. mutans* viviparous, and Railliet figures *gallinae* ♀ with obvious larvae inside.

♀ 408–440μ × 330–380μ; very short oval; abdomen (at first) as large as cephalothorax; rostrum with very broad carinate cheeks, filling the interval between legs 1 and head; dorsum mammillated; transverse tocostome just behind epimeres of legs 2; legs reduced to short conical stumps without ambulacra.

This sarcopt has been known for a long time on domestic fowls and other Gallinaceae and on game birds. It has also been observed to infest small birds in aviaries. It burrows under the scales of the legs and causes large spongy crusts which are full of the mites.

Note the absence of "cheeks" in the ♂, and the presence of very broad well-developed cheeks in the ♀.



Text-figure 10. *Cnemidocoptes laevis* var. *gallinae*, ♂ × 200 (after Railliet).

C. laevis Railliet, 1885.

Railliet (1895, p. 664) describes it thus:

Rostrum broad, half covered by the epistome; ♂ oval, without cheeks; genital armature between legs 4; two copulatory suckers one on either side of the anus.

♀ rounded; abdomen a little larger than cephalothorax; cheeks as in *mutans*; dorsum regularly striate, without mammillae; tocostome faint; legs as in *mutans*.

This species causes "body" or "depluming" scabies, and was first found on a carrier pigeon from Brussels. Railliet says it appears in poultry yards in consequence of the introduction of infested fowls and quickly invades the whole run. It usually begins on the rump and spreads to thighs, back and belly, and the feathers fall off. The fowls do not usually suffer much in health,

but deteriorate in flesh and in egg-laying. Cocks suffer most, and sometimes die in a cachectic state. The disease is most prevalent in spring and summer.

The varieties of *laevis* which have been founded by various writers are:

Fossor Ehlers, 1873, on the passerine bird *Munia maja*, and *glaberrimus* and *philomelae* described by Sicher, 1893, from *Dendrocopus medius* and *Luscinia philomela* respectively.

Railliet's type species is sometimes known as *C. laevis* var. *gallinae*. Ehlers (1873, "Die Krätzmilben der Vögel," *Zeitschr. f. wiss. Zool.*, pp. 228–253, Pls. XII and XIII) gives beautiful figures of *fossor* (under the genus *Dermatoryctes*). Its chief characteristic is the possession of four claws on the female tarsus. The epimeres of legs 1 are free.

Sicher (1893, pp. 134 *et seq.*) describes *glaberrimus* and *philomelae*:

Glaberrimus has the epimeres of legs 1 free, and no posterior hairs; in *philomelae* the epimeres of legs 1 meet at an obtuse angle, and there are six hairs of about equal length at the posterior end of the body.

The males are not known.

CONCLUSIONS.

We have little doubt that future investigators will regard *Sarcoptes*, *Notoedres* and *Cnemidocoptes* as generically distinct. *Cnemidocoptes*, always parasitic on birds, and comprising members of different habits—scab forming or depluming—would seem to form a compact group for a separate research. *Notoedres*, attacking small mammals, but often communicated by them to the larger mammalia and to man, cannot well be dissociated from *Sarcoptes* in any study of the acarine causes of scabies, but the foregoing résumé of our present knowledge of the subject makes it abundantly clear that the urgent and immediate need is to clear up the confusion which exists with regard to the last-named genus. Whether different forms are to be regarded as species, varieties or races is, after all, a minor matter, and one as to which differences of opinion may well continue to exist after the most thorough investigation. What is important is that one form should be so completely studied that differences of structure in forms thought to be distinct from it may be clearly recognised, and when this has once been accomplished a foundation will at least have been laid for a comparison between the *Sarcoptes* of the different animals. The human *Sarcoptes* would probably be selected for this purpose. If so, care should be taken that the patients who supply the material should not be men occupied in the tending of domestic animals, and especially of horses, lest there be any suspicion of contagion from such sources. There would be some advantages in selecting instead the form known as *equi*, which is easily obtainable, and in which the salient characteristics would seem to be more strongly marked.

Any structural peculiarity which has been noted in *any* so-called species or variety should be specially looked for in the type selected for exhaustive study, Mégnin's experience being always borne in mind. He made a new

species based on characters which, when deliberately sought for, were found to be present in all the forms he was able to examine.

Chaetotaxy is always important in the Acarina, and should be studied with especial care. The bristles and hairs are difficult to see in a transparent medium, and particularly so in Canada balsam which has nearly the same refractive index. It is absolutely necessary to examine them in some medium which shall render them more visible. It will be noticed that in the Plate the hairs of Munro's figures of *S. scabiei* are much longer than those depicted by any other investigator, and this is entirely due to his viewing them in a gum-arabic medium. It is possible that picric acid or some other reagent might stain them faintly, and there is a third method—of viewing the specimen in a coloured field of some colloid pigment, when unsuspected length of bristles is often betrayed by the length of the light tracts traced by them on the coloured background. The particular distribution and the comparative length of these bristles would, if constant, be good specific characters.

The observations of Fürstenberg and others on the dorsal scales, the notothoracic cones and the notogastral spines should be repeated and extended. If, for example, Fürstenberg is accurate in his delineation of the dorsal scales of the sarcopt of man and of the sarcopt of the dog there can be no doubt that these two forms are essentially distinct.

The leg armature and chitinous frame-work, and the epimeres should once more be subjected to a very close scrutiny. Fürstenberg and others have delineated the skeletal structures of the legs under a high magnification, and with considerable detail of structure. Nevertheless it will be noted that not a single one of the best accredited figures of the human sarcopt shows the presence of a trochantal claw on the anterior legs. Canestrini figures it very clearly in the case of two other "species" (*e.g.* see Canestrini, VI. Pl. 60) and Mégnin detected it in a horse sarcopt which he judged to be a new species—largely on account of its presence. When, however, he re-examined the human *Sarcoptes* for the express purpose of finding it he was at once successful. In fact he was driven to the conclusion that it was a constant feature of all the forms of *Sarcoptes*.

If there are real specific differences between the various forms of *Sarcoptes*, one would expect them to be indicated in their most fixed, and strongly chitinised structures, the epimeres. Slight differences are alleged to exist in these epimeres, especially those of the second pair of legs, which are sometimes nearly straight, at others sharply bent outwards at their free extremities. Their extremities, also, may present useful differences, and be knobbed or forked as the case may be. All these details will naturally engage the attention of anyone undertaking a revision of the subject.

In the diagnoses of the various forms mention is generally made of certain clear areas (clairières, Blösse), on the dorsum. It appears to me that the terms are used in a double sense, sometimes indicating simply a region where the striations are absent (as on the notogaster of the female), but more often

used to denote a definite area with a granular or rugose surface and sometimes more distinctly chitinised than the rest of the integument. These are what Munro calls "rugose areas" and what he very diagrammatically depicts as dark patches, one on the notothorax of both ♂ and ♀, and two on the notogaster of the ♂. Mégnin says that in *equi* the notothoracic rugose area (plastron) is of a faint yellow colour. In the human sarcopt it seems to be very inconspicuous, and it does not appear at all in many of the best accredited figures of this form. Gerlach shows it as a bare, somewhat rectangular light patch. It is present in all the varieties, and may perhaps be regarded as a sort of rudimentary scutum, such as is found in many arachnids. Its shape and dimensions are considered to be of taxonomic importance, and indeed, if it be of the nature of a scutum, it is just one of those structures in which forms which are really distinct might be expected to exhibit differences.

In the Acarina for the most part the males of the various species are more distinctive than the females. So far, in the genus *Sarcoptes*, only very slight differences between the males of the various forms have been noted, the most important being the relation of the epimeres of the posterior legs to the epiandrium. The smaller size, and the relatively small number of the males, may have militated against their receiving due attention, but if they are all as similar as the various observers have apparently found them this would certainly argue a very close affinity between the different forms of *Sarcoptes*.

When once the chaetotaxy and armature of a single form have been definitely established, *Sarcoptes* taken from characteristic cases of scabies in other animals may be compared with it as occasion arises. All possible care must again be taken that the case shall be one of the ordinary scabies of the animal, and not a temporary infection from an animal of a different group.

Much reliance has been placed upon mere size. When the very wide range given in the measurements of the adult female and male of all the so-called species is considered, it is not easy to believe in the great importance of this character. It would at most indicate a distinction of race in the absence of more significant differences of structure. Some writers have arranged the varieties they recognise in order of size. Dubreuilh and Beille, for instance (p. 12), give as a descending series *suis*, *equi*, *lupi*, *caprae*, *cameli* (our *dromedarii*), *ovis* and *hominis*, the first-named attaining 500μ in length and the last 300μ. It is admitted that, notwithstanding considerable inequality in the size of individuals, there may still be a noticeable difference in average size in the forms found on different hosts. Care should at least be taken that the average size attributed to any form be based on the measurement of a sufficient number of specimens. Where transference from one animal to another is possible it would be a very interesting observation to note whether it is accompanied by any change in average size.

The proposed research will no doubt include experiments in the artificial transference of scabies from one animal to another, and the views—and the warnings—of Delafond and Bourguignon in this connection will be especially

interesting, whatever the final verdict may be concerning them. They regarded the domestic animals as the constant reservoir from which man renewed his supply of *Sarcoptes*, which would otherwise have been exterminated by its very easy treatment. They believed that for scabies to flourish in any of the lower mammalia a poor condition of health was necessary, and that man, and perhaps monkeys, are the only exceptions to this rule. And they warn us repeatedly against drawing any conclusions from failure to communicate scabies to another animal by the transference of a limited number of possibly injured *Sarcoptes* from a given host.

In all the cases in which severe scabies has been successfully and quickly communicated to a different animal the first host has been in an advanced stage of the disease, exhibiting crusts which are swarming with the mites in all stages. Contagion from animals only slightly affected by scabies is always slow and uncertain. Human scabies (except in the form of Norwegian itch) is almost always relatively slight, presenting no crusts, and it is notorious that doctors never contract itch from their patients, and that even when a man has become infected from occupying the bed of a scabietic person weeks may elapse before he becomes aware of the fact. Again it very often happens in these experiments that the transference is successful for a time but that the disease presently dies out. The possible explanation that the recipient host is in a condition of health unfavourable to the establishment of the disease must not be lost sight of. It was not till the bear and the hyaena in the Ménagerie Pianet had greatly lost condition from other causes, that they contracted scabies from the mangy lions, and many parallel cases have been recorded.

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DESCRIPTION OF PLATE XV.

Figures of *S. scabiei* de Geer given by different investigators from 1687 to 1919.

Fig. 1. Bonomo's (? Cestoni's) figure, regarded as the classical representation of the mite from 1687 to 1750. (From Raspail, 1838, Pl. XV, fig. 14.)

Figs. 2 and 3. Linnaeus' figures of *Acarus exulcerans* and *A. scabiei* according to Wichmann. (From Raspail, 1834-46, p. 111.)

Fig. 4. De Geer's figure, 1778. (From Raspail, 1838, Pl. XV, fig. 11.)

Fig. 5. The mite as seen by Raspail. (Raspail, 1838, Pl. XV, fig. 1.)

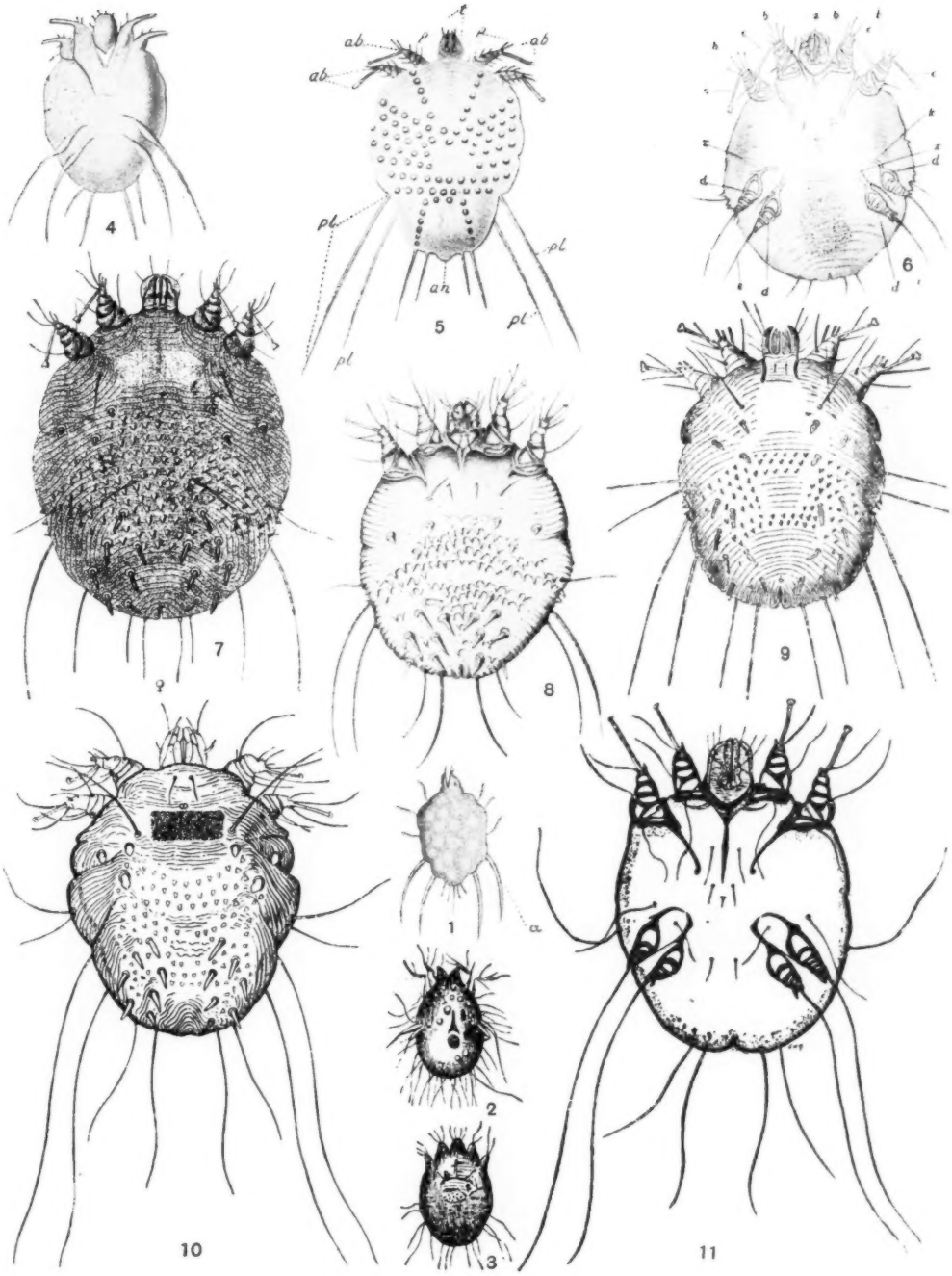
Fig. 6. Delaford and Bourguignon's figure (*Traité pratique*, Pl. I, fig. 1), practically a reproduction of Bourguignon's figure of 1852.

Fig. 7. Gerlach's figure, 1857. (Gerlach, Pl. I, fig. 1.)

Fig. 8. The mite according to Fürstenberg, 1861. (Fürstenberg, Pl. I, fig. 7.)

Fig. 9. Blanchard's figure, 1889. (From Brumpt, fig. 322.)

Figs. 10 and 11. Dorsal and ventral aspects of *S. scabiei* according to Munro, 1919. (Munro, figs. 1 and 2.)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A CONTRIBUTION TO OUR KNOWLEDGE OF THE TAPEWORMS OF POULTRY.

By F. J. MEGGITT, M.Sc., Ph.D.,

Assistant Helminthologist, University of Birmingham.

(*From the Research Laboratory in Agricultural Zoology, University of Birmingham.*)

(With Plate XVI and Plate XVII, Figs. 8–11, and 1 Text-figure.)

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The following paper is an account of the results obtained by the study of Cestodes sent to this Department for identification. For the most part, the tapeworms were species with a wide distribution and with many previous records of their occurrence. Among them were several whose anatomy, well-known in many respects, had been inadequately described with regard to characters useful, if not essential, for identification.

The present paper, with the exception of that portion concerning the new species *Cotugnia fastigata*, is an attempt to deal with such characters and so complete already existing descriptions.

I wish here to express my indebtedness to Prof. Nuttall, F.R.S., for specimens of *Hymenolepis columbae* (Zed.), *H. coronula* (Duj.), *H. gracilis* (Zed.), and *Cotugnia fastigata* n. sp., collected by Dr H. H. Marshall at Rangoon, and to Dr C. L. Boulenger for those of *Cotugnia digonophora* (Pasq.), from Mesopotamia.

COTUGNIA DIGONOPHORA (Pasquale, 1890).

The genus *Cotugnia* was created by Diamare (1893) for those avian Cestodes which have a double set of male and female reproductive organs in each proglottis, and a rostellum armed with T-shaped hooks. The type species is *C. digonophora* (Pasq.), a form described under the name of *Taenia digonophora* by Pasquale in 1890 from chickens in Abyssinia. Since that date,

with the exception of a paper by Khitrow (1900) inaccessible to me, the species has not been recorded. Pasquale's description is incomplete in many respects so that, although through the work of Fuhrmann (1909) on the species *C. crassa* Fuhr., *C. collini* Fuhr. and *C. polycantha* Fuhr., the genus is well defined, the type species has remained practically undescribed. Three complete tapeworms from chickens in Mesopotamia were handed to me for identification. These I believe to be specimens of *C. digonophora* (Pasq.), and take the opportunity to compile as full an account as possible of the anatomy of this type species.

The sizes of the strobilae are 107 mm. × 4 mm., 80 mm. × 4 mm., 26 mm. × 2·5 mm. and 22 mm. × 2·5 mm. The scolex (Pl. XVII, fig. 9) is 0·66 mm. long × 1·07 mm. broad, with four unarmed suckers 0·36 mm. long × 0·25 mm. wide, arranged two dorsally and two ventrally. The rostellum is 0·16 mm. in diameter, armed with a double crown of hooks 0·0122 mm. long, of the usual *Davainea* shape, the hooks on each row being of the same size and alternating with each other, with but little difference in their anterior level. The rostellum itself is a simple muscular structure sunk between four large lobes which completely hide it. All proglottides are broader than long.

These measurements do not agree with those quoted by Stiles (1896, p. 30) "Strobila 40 mm. to 80 mm. by 8 mm. broad and in contracted condition about 1 mm. thick; head 1·4 mm. by 1·12 mm., rostellum with a crowded crown (in a single row) of very small hooks 8·35μ long; base of rostellum 0·22 mm. by 0·15 mm., suckers globular, prominent, 0·35 mm. in diameter. Neck short. Anterior segments broader than long, posterior segments longer than broad. Genital pores double in about the middle of the lateral margins; two ovaries in each segment; eggs evidently arranged in egg sacs."

These differences in the measurements and the shape of the proglottides, characters indefinite and liable to variation, are probably the result of individual variation in the tapeworms examined and can therefore be safely neglected.

The longitudinal musculature (Pl. XVII, fig. 11) is in two layers. The innermost (*l.m.*) consists of numerous bundles of loosely packed fibres, approximately 20 fibres to a bundle. Internally it is bounded by a single (*t.m.*) and externally by a double (*t'.m'.*) layer of transverse muscles, the two layers of the latter separated by a narrow stratum of parenchyma. Numerous dorsoventral fibres cross these two last layers and pass between the inner longitudinal muscle bundles. Externally to the transverse muscles mentioned is a widely diffused layer of longitudinal muscles (*l'.m'.*). Internally these form very compact bundles of very few fibres, approximately 10 per bundle, but diminish gradually to isolated fibres which do not extend as far as the cuticle. Both these two longitudinal muscle layers extend posteriorly into segments containing mature eggs, but only the inner extends anteriorly into the scolex. There it is much stronger, the bundles being more numerous and more compact, and forming an almost continuous layer which ceases at the posterior half of the suckers.

The excretory system consists of the usual four longitudinal vessels, two dorsal and two ventral. The former are exceedingly minute and are external to the two latter. At the posterior limit of each proglottis, the two ventral vessels communicate by a large transverse commissure. No such commissure could be found between the two dorsal, probably on account of their small size. In segments filled with mature eggs, both dorsal and ventral vessels disappear. In the anterior segments they are of equal size. In the scolex they run between the suckers in a wavy course, giving off numerous anastomosing branches and opening into a circular commissure, immediately posterior to the rostellum.

There are two complete sets of genital organs in each proglottis (Pl. XVII, fig. 10). The genital pore is half way along each lateral margin or else slightly anterior. A very shallow genital cloaca is present. The genital canals run dorsal to both excretory vessels and to the nerve.

The cirrus-pouch is long and slender and devoid of special retractor muscles. It only extends as far as the nerve, not past it as Fuhrmann (1909, p. 120) states, "Der Cirrusbeutel ist langgestreckt (0·3 mm.) und geht über den Längsnerv bis zu dem nach aussen vom ventralen Exkretionsstamm gelegenendorsalen Exkretionsgefäss," and is straight. The cirrus is armed with fine spines and has a small terminal enlargement. It runs in a straight line half-way along the cirrus-pouch and then merges into the vas deferens; after this point the cirrus-pouch is less muscular. The vas deferens is twice the diameter of the cirrus and is uncoiled while still within the pouch. On emerging, it coils into a loose ball and then, running posteriorly, breaks up into the vasa efferentia. There is no vesicula seminalis, the coils of the vas deferens functioning instead. The testes (*t.*) form a broad band across the proglottis, are approximately 100 in number and are posterior to the female glands. None are to be found in the anterior half of the segment. They surround dorsally and laterally, but not ventrally, the longitudinal excretory canal and extend as far as the longitudinal nerve. Dorso-ventrally they form an indistinct double layer in the centre of the proglottis, being three deep at the extremities and only one deep in the centre.

The vagina (*v.*) opens posteriorly to the cirrus and runs slightly posteriorly to open into a spindle-shaped receptaculum seminis (*r.s.*) situated just internally to the excretory vessels. The ducts from the receptaculum seminis take their usual course. The ovary (*ov.*) is crescent shaped with the concavity directed posteriorly and internally, and with the convex side deeply lobed. The yolk-gland (*y.g.*) is a shapeless irregularly lobed gland lying posteriorly and internally to the ovary. Both ovary and yolk-gland lie immediately internally to the longitudinal excretory vessels with the ovary half-way between the posterior and anterior borders of the segment. The shell-gland is very compact, non-lobed, and lies on the dorsal surface between the ovary and yolk-gland. A definite uterus is not developed. The oviduct, after passing through the shell-gland, persists for an exceedingly short distance

as a rather wide indistinct parenchymatous tube filled with eggs and ends blindly in the parenchyma. In a proglottis at this stage of development the anterior half is already full of fertilised eggs; in the stage immediately preceding, the uterine tube has more definite walls but still ends blindly, while but few eggs are visible in the proglottis. In proglottides ready for detachment, the eggs fill the entire segment, extending laterally to the excretory vessels almost to the margin of the segment. Adjacent proglottides are separated only by a thin plate of parenchyma. The egg is ellipsoidal, measuring 0·63 mm. × 0·583 mm. and the onchosphere 0·288 mm. × 0·249 mm.

COTUGNIA BROTOGERYS (Meggitt, 1915).

This species from a parakeet, *Brotogerys tirica*, has already been described in detail (Meggitt, 1915). Revision of the material has recently shown that this description is inaccurate in one respect. It has been stated (p. 54) that the parenchymatous capsules each contain several ova. This is not correct. In young segments the eggs lie singly in separate capsules. As the proglottis matures the number of eggs increases and the capsules become packed so closely together that in many cases the walls separating them disappear. The capsules thus appear each to contain several ova.

The testes surround the longitudinal excretory vessel except on the dorsal surface, a condition exactly opposite to that in *C. digonophora*. Anteroposteriorly, the band of testes consists of five rows; dorso-ventrally they lie in the centre of the proglottis.

COTUGNIA FASTIGATA n. sp.

Amongst a large number of *H. coronula* (Duj.) from domestic ducks, Rangoon, were found several complete specimens of a *Cotugnia*. Upon examination these proved to represent a new species for which I propose the name *Cotugnia fastigata* n. sp. and which may be identified by the key attached to the following description.

The length is 30 mm., the breadth 6 mm., and all the proglottides are broader than long. In shape the strobila (Pl. XVI, fig. 4) is triangular, widest at the base and narrowing gradually towards the head. The scolex is 0·5–0·6 mm. diameter, and is provided with four unarmed suckers and an armed rostellum. The latter is 0·29 mm. diameter, and bears approximately 200 hooks, 0·02 mm. long, arranged in a double row, the hooks of the two rows alternating. It proved impossible to ascertain the exact shape of the hooks owing to the difficulty of isolating them; one figured in Text-fig. 1 is from a section and has obviously been cut at the place marked *x*. The base of each hook (Pl. XVII, fig. 8) has a fine sheath of muscle (*m.*) surrounding it. Posteriorly this merges into a fine muscle strand 0·5μ diameter which, uniting with adjacent muscle strands, ultimately joins the body longitudinal muscles. Externally to the hooks and surrounding the rostellum is a thin sheath of transverse muscles.

The scolex (Pl. XVI, fig. 7) is attached to several villi which, free at first, in course of time become fused together into a solid mass at their distal ends but with the proximal ends still showing traces of their original formation. To this thickened lump the scolex fixes itself by the rostellor hooks. The centre of the rostellum, instead of being applied closely to the mass of villi, retracts, so as to leave between the scolex and the intestine a conical cavity, often partially filled with mucous, round the circumference of whose base the rostellum is still firmly fixed by its hooks. The suckers appear to play a temporary part in the fixation of the worm to the intestine; immediately on death they relax their hold while the rostellum generally remains firmly imbedded. The scolex may hang freely in the lumen of the intestine or may be sunk among the villi, but it never penetrates the submucosa.

Text-fig. 1. *Cotugnia fastigata* n. sp., Hook from Rostellum.

The musculature (Pl. XVI, fig. 6) consists of three layers of longitudinal muscles each bounded internally by a thin layer of transverse ones. The innermost longitudinal musculature (*l.m.*) consists of a number of fibres aggregated together into large irregular bundles; the bundles of the middle layer (*l'.m'.*) are smaller, more compact, composed of fewer fibres, and arranged more regularly, while externally to them isolated fibres (*l''.m''.*) extend up to the cuticula.

The dorsal longitudinal excretory vessels are absent from proglottides containing genital organs; the ventral persist to the posterior end of the strobilus, and communicate by the usual transverse commissure at the posterior border of each proglottis.

The genital pore (Pl. XVI, fig. 5) is situated at the limit of the anterior quarter of the proglottis margin, and into it open anteriorly and posteriorly the cirrus-sac and vagina respectively.

The testes (*t.*) extend as a narrow band along the posterior border of the proglottis. Antero-posteriorly, this band has a uniform width, consisting of two to three rows of testes; dorso-ventrally, it is thickest laterally where

there are three layers of testes extending from the dorsal to the ventral surface and thinnest in the centre where there is only a single layer on the dorsal surface. Laterally the testes surround the ventral excretory canal and extend as far as the nerve. There is also a small group of testes situated between the ovary and the excretory canal. The anterior portion of the proglottis is entirely free from them. The cirrus-sac (*c.s.*) is small and narrow but long in proportion to its width, and extends as far as the lateral nerve. Between it and the testes, the vas deferens forms a closely packed bundle of coils surrounded by numerous gland cells. Inside the sac, the vas deferens coils once or twice and then opens into the short straight cirrus.

The vagina runs in a straight course laterally to open into a small spindle-shaped receptaculum seminis (*r.s.*). The ovary (*ov.*) is deeply divided into several blunt lobes closely packed together. It lies posterior and ventral to the receptaculum seminis and close to the excretory canal. Posterior and slightly aporal to it is the compact yolk-gland (*y.g.*) surrounded laterally by the testes.

The uterus (*u.*) is present as a narrow branched tube anterior to the ovary, but soon disappears, the mature eggs lying singly in capsules in the parenchyma.

KEY TO SPECIES OF COTUGNIA.

1.	Rostellum smaller than suckers	*C. margareta* Beddard
	Rostellum larger than suckers	(2)
2.	Testes 6–7, anterior to female glands	*C. browni* Smith
	Testes numerous, lateral or posterior to female glands	(3)
3.	Testes clearly divided into two lateral groups	(4)
	Testes in one broad posterior band	(5)
4.	Testes in one layer transversely	*C. collini* Fuhr.
	Testes in several layers transversely	*C. polycantha* Fuhr.
5.	Cirrus-sac extending beyond ventral longitudinal excretory vessel	*C. fuhrmanni* Bacz.
	Cirrus-sac not reaching ventral longitudinal excretory vessel ...	(6)
6.	Yolk-gland lateral to ovary	*C. crassa* Fuhr.
	Yolk-gland posterior to ovary	(7)
7.	Testes 2–3 rows antero-posteriorly	*C. fastigata* n. sp.
	Testes 5 rows antero-posteriorly	(8)
8.	Testes dorsal and lateral to longitudinal excretory vessels ...	*C. digonophora* (Pasq.)
	Testes ventral and lateral to longitudinal excretory vessels ...	*C. brotogerys* Meggitt

(*C. inaequalis* Fuhrmann 1909 has not been described sufficiently to allow of its inclusion in this table.)

HYMENOLEPIS COLUMBAE (ZEDER, 1800).

The specimens of this species had been collected from pigeons, Rangoon, and consisted of portions of strobila in various stages of development. No scoleces were found. According to Ransom (1909, p. 97) this species is identical with the *H. sphenocephala* (Rud.) described by Fuhrmann (1906, p. 449), whose description, with the exception of the points mentioned below, was fully corroborated by my preparations.

The genital pore is much more anterior than is figured by him, lying in the anterior quarter of the proglottis; the genital cloaca is also much shallower, being only a small depression. The vagina consists of two separate parts. The first, muscular and with an extremely wide lumen, runs dorsally from the genital cloaca as far as the inner limit of the sacculus accessorius, there to open into a more muscular duct with no apparent lumen. This latter portion is spirally coiled, and runs ventrally and anteriorly to open into the receptaculum seminis. The difference between the two parts of the vagina is very marked. Of the two aporal testes, Fuhrmann (1906 *a*, p. 450) states "der vordere (liegt) aber etwas ausserhalb des hinteren antiporalen Hodens." Preparations and sections showed this clearly. Though the two testes often appeared to lie one directly anterior to the other, yet in every case a projecting tongue from the anterior one lay external to the posterior, and a distinction between internal and external could be made.

HYMENOLEPIS CORONULA (DUJARDIN, 1845).

This cestode of ducks has been described by many authors, in particular by Wolffhügel (1900, p. 165), but although most of its anatomy is well-known the following points have escaped attention. The specimens I received were taken from domestic ducks in Rangoon.

The three testes (Pl. XVI, fig. 1, *t.*) are arranged as Fuhrmann (1906 *a*, p. 733) states, one poral and two aporal, the edges of the poral and the inner aporal testes touching in young segments but being gradually separated by the growth of the female glands between them. The arrangement of the two aporal testes varies according to the state of contraction of the segment; in proglottides extremely contracted, as in the one figured, the three testes are in the same straight line; in proglottides extended, one aporal testis lies anterior to and internal to the other. In all cases though, the outer testis has a small projection lying posteriorly to the inner, so that even when in the same straight line a distinction into anterior testes and posterior testis can be made. Wolffhügel (p. 171) states, "Die drei Hoden erreichen bei *Dicranotaenia coronula* in höchster Reife eine solche Grösse, dass sie bis an die dorsale und ventrale Längsmuskulatur stossen." This I have not found to be the case, the three testes lying well within the musculature. The cirrus-sac (*c.s.*) extends as far as, or just passes, the ventral longitudinal excretory vessel, and is two-thirds filled by the internal vesicula seminalis (*v'.s'.*), rather a larger proportion than figured by Wolffhügel (Pl. VII, fig. 103). The cirrus extending from this vesicula seminalis to the genital pore is straight and the small sacculus accessorius present is a straight tube of uniform diameter with no terminal enlargement; both these observations do not agree with the figure above mentioned. The external vesicula seminalis (*v.s.*) is small, and spindle shaped, and lies dorsal and lateral to the receptaculum seminis.

The female glands (Pl. XVI, fig. 2) are posterior and ventral, and occupy one-third of the proglottis breadth. The bluntly lobed yolk-gland (*y.g.*) lies

on the posterior and ventral surface of the segment and is surrounded on all sides except the posterior by the narrow unlobed ovary (*ov.*).

When fully developed, the receptaculum seminis (*r.s.*) extends from the ventral longitudinal excretory vessel to a little over half-way across the segment. It is slightly funnel-shaped, the inner end being rather larger than the outer. The uterus (*u.*) in its early stages is a long narrow sac twisted upon itself so that its cavity appears to be divided by septa. Later it increases in size and occupies the whole of the proglottis, extending past the excretory vessel as far as the cuticula. At this stage the proglottis is a mere egg-sac, but with no communication with adjacent segments. As was the case with other observers, no mature eggs could be found.

HYMENOLEPIS GRACILIS (ZEDER, 1803).

The specimens of this species were obtained from the intestine of domestic ducks, Rangoon, and sections confirm Wolffhügel's account. The following additional points were noticed. The genital pore (Pl. XVI, fig. 3, *g.p.*) is extremely anterior, in the anterior quarter of the proglottis margin, and is often covered by the overlapping of the preceding segment. The cirrus-sac (*c.s.*) does not, as Lühe (1910, p. 61) states, barely reach the centre line of the proglottis, but extends well past it, nearly to the aporal longitudinal excretory vessel. The testes (*t.*) are arranged as Fuhrmann (1906 *b*, p. 733) states, one poral and two aporal; of the latter the one is always external and anterior to the other. As stated by other investigators no transverse commissures could be traced between the longitudinal excretory vessels of opposite sides. A large number of minute branches are given off during their course, particularly in the neighbourhood of the posterior margin of the proglottis and as these latter branches penetrate some distance into the segment and could often be traced half-way across it, it is a reasonable supposition that through them the opposite excretory vessels communicate.

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For description of Plates XVI and XVII see p. 313.

A NEW SPECIES OF CESTODE (*OOCHORISTICA ERINACEI*) FROM THE HEDGEHOG.

By F. J. MEGGITT, M.Sc., Ph.D.,

Assistant Helminthologist, University of Birmingham.

(*From the Research Laboratory in Agricultural Zoology, University of Birmingham.*)

(With Plate XVII, Figs. 12–13.)

A number of Cestodes collected from a hedgehog in Mesopotamia by Dr Boulenger were handed to me for identification. Examination showed them to belong to the genus *Oochoristica*. Five Cestodes [*Hymenolepis erinacei* (Gm.), *Hymenolepis steudeneri* v. Janicki, *Davainea parva* v. Janicki, *Taenia voluta* v. Linstow, and a *Bothriocephalus* larva v. Janicki] have up to the present been recorded from this host. From all these, the present species is distinguished by its possession of numerous testes, situated posteriorly to the female organs. I therefore propose to form a new species for its reception and suggest for it the name *Oochoristica erinacei*. The key attached to the following description will serve to distinguish this new species from others of the same genus. I wish here to express my indebtedness to Dr Boulenger for placing his material at my disposal.

The length of the largest specimen is 15 mm. and the width 1 mm. The scolex (Pl. XVII, fig. 12) is 0·33 mm. diameter, provided with four suckers 0·165 mm. long × 0·12 mm. broad, arranged in pairs, the members of each pair having their margins touching and being widely separated from the opposite pair. Anteriorly each sucker has a small opening leading to a slight furrow on the apex of the scolex, the whole having a similar appearance to that figured by Cohn (1903, p. 61, Text-fig. 6) for *O. surinamensis*. There is neither rostellum nor hooks. A neck is absent, segmentation starting immediately posteriorly to the suckers.

As figured by Beddard for *O. marmosae* (1914, Text-fig. 149) the strobilus swells out into a collar immediately posteriorly to the scolex. The musculature consists of an inner layer of transverse muscles, externally a layer of comparatively strong longitudinal ones, and externally to those a very weak layer of scattered fibres, only present in the more anterior segments and disappearing in those with fully developed genital organs.

There are the usual four longitudinal canals, two ventral and two dorsal, communicating by a circular commissure at the posterior end of each proglottis. The two dorsal are small, and the two ventral relatively large, the commissures connecting the latter being often one-third the dorso-ventral diameter of the proglottis. Besides these four vessels there is an extensive irregular meshwork of ill-defined vessels and lacunae. Of the additional longitudinal vessels described by investigators and stated to be characteristic of the genus I have been unable to find any trace. The network referred to above is of far too vague a character to correspond in any way with a definite system such as is to be found in the other species, *e.g. O. tetragonocephala* (Bremser).

The genital pore (Pl. XVII, fig. 13) irregularly alternates and is situated near the anterior extremity of the proglottis. It leads into a well-developed genital cloaca into which the vagina and cirrus open in the usual manner. The genital ducts pass between the dorsal and ventral excretory vessels and dorsal to the nerve. The male organs are fully developed in proglottides slightly broader than long, the female in those longer than broad. The cirrus-sac (*c.s.*) opens into the genital cloaca dorsally to the vagina. Lying diagonally, it extends well past the ventral longitudinal vessel, in some cases half-way across the segment. The cirrus is unarmed, has a small terminal knob, and coils slightly in the cirrus-sac. The vas deferens inside the sac is also coiled. It leaves the cirrus-pouch at the inner extremity on the ventral side, and, coiling once or twice, proceeds half-way across the proglottis near the dorsal surface, immediately dorsal to the uterus but not passing between the lobes of the ovary. At the level of the anterior extremity of the vitelline gland it breaks up into a number of vasa efferentia. The testes (*t.*) are between 30–50 in number and lie posteriorly and laterally to the female glands, not extending anteriorly further than the ovary. They form one layer dorso-ventrally and do not extend laterally beyond the longitudinal excretory vessels.

The vagina (*v.*) opens at the posterior limit of the genital cloaca and runs transversely to half-way between the two ventral longitudinal vessels. After coiling once or twice it opens into the oviduct in the centre of the proglottis. A receptaculum seminis is not present. The bilobed ovary (*ov.*) is situated in the anterior third of the proglottis, the basal portion being dorsal and the two lobes reaching the ventral side. Between these two lobes lie the greater part of the courses of the vagina, uterus, and oviduct. The latter springs from the ventral surface of the common basal portion of the ovary and proceeds in a straight line posteriorly to meet the vagina. From this meeting place the oviduct curves first posteriorly, then anteriorly to the ventral surface of the proglottis, receiving at the posterior limit of its course the vitelline duct. On the ventral surface it runs anteriorly past the level of the vaginal pore, then bends at right angles to run across the segment to the dorsal surface where it opens into the uterus. The yolk-gland (*y.g.*) lies

posteriorly to the centre of the proglottis, half-way between dorsal and ventral surfaces. It is bilobed, the lobes being directed anteriorly. The vitelline duct arises from the common posterior basal portion and runs anteriorly, at first on the ventral surface, later crossing the segment to open in the centre into the oviduct.

At its first appearance the uterus is an amorphous sac situated anteriorly and, in a transverse section through that region, occupying the whole of the proglottis. As it develops it extends posteriorly and sends out numbers of branches which ramify in all directions. This process continues, the whole uterus resolving itself into a meshwork of tubes; these ultimately form capsules containing at first several, but later only a single egg.

Key to Species of Oochoristica.

1.	Egg-capsules contain several eggs	*O. megastoma* (Dies.)
	Egg-capsules contain only one egg	(2)
2.	Testes extend anteriorly to ovary	(3)
	Testes posterior, or lateral and posterior to ovary ...	(4)
3.	Host, *Amphisbaena alba*	*O. amphisbaena* (Rud.)
	Host, *Zonurus tropidosternum*	*O. zonuri* Bayliss
4.	Vagina opens anteriorly to cirrus	(5)
	Vagina opens posteriorly to cirrus	(6)
5.	Genital ducts pass between longitudinal excretory vessels	*O. tetragonocephala* (Brem.)
	Genital ducts pass dorsally to longitudinal excretory vessels	*O. didelphydis* (Rud.)
6.	Testes lateral and posterior to ovary	(7)
	Testes posterior to ovary	(11)
7.	Rostellum absent	*O. cryptobothrium* (v. Linstow)
	Rostellum present	(8)
8.	Testes 50	*O. incisa* Marotel
	Testes 100 or more	(9)
9.	Cirrus-sac not reaching outer longitudinal excretory vessel	*O. marmosae* Bedd.
	Cirrus-sac reaching or passing outer longitudinal excretory vessel...	(10)
10.	Genital ducts pass between longitudinal excretory vessels	*O. rostellata* Zsch.
	Genital ducts pass dorsally to longitudinal excretory vessels	*O. surinamensis* Cohn
11.	Eggs absent from centre of proglottis	*O. bivittata* v. Jan.
	Eggs present in centre of proglottis...	(12)
12.	Testes 15–20	*O. tuberculata* (Krabbe)
	Testes 20–30	*O. truncata* (Rud.)
	Testes over 30	(13)
13.	Receptaculum seminis present	(14)
	Receptaculum seminis absent	(15)
14.	Testes 39–46	*O. agamae* Bayliss
	Testes 70–80	*O. wagneri* v. Jan.
15.	Eight longitudinal excretory vessels	*O. sp* Beddard
	Four „ „ „	*O. erinacei* n. sp.

(*Oochoristica pseudopodia* (Krabbe), *O. murina* (Rud.), and *O. sp*? von Janicki 1906, are not included in the above key, their anatomy not having been sufficiently investigated.)

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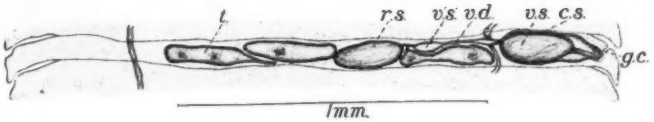

Fig. 1

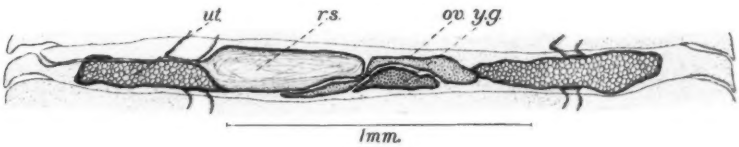

Fig. 2

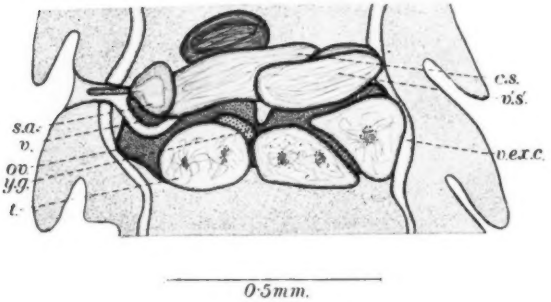

Fig. 3

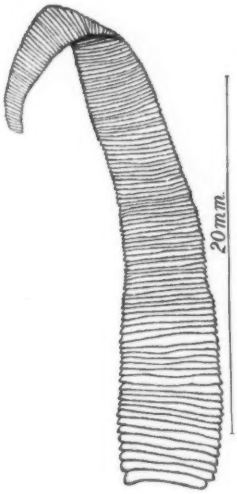

Fig. 4

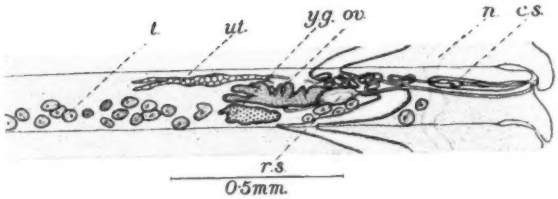

Fig. 5

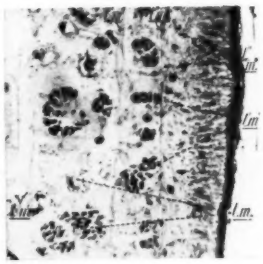

Fig. 6

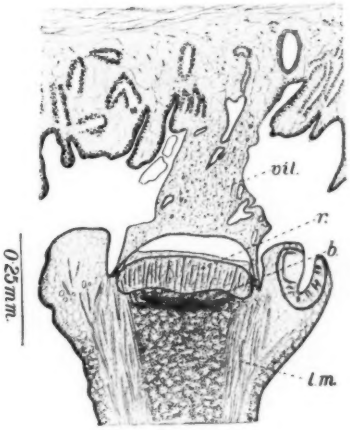

Fig. 7

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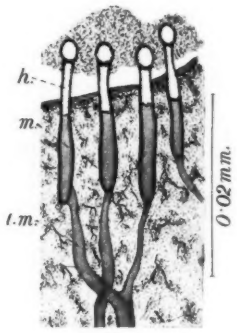

Fig. 8

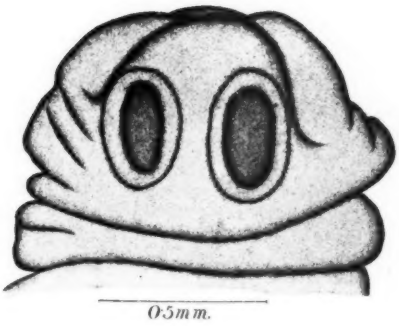

Fig. 9

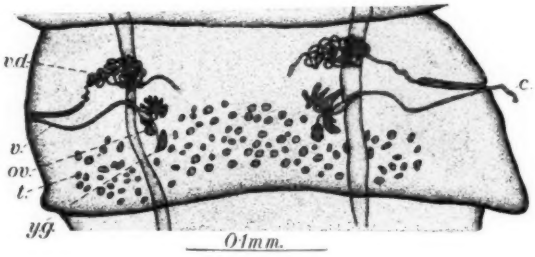

Fig. 10

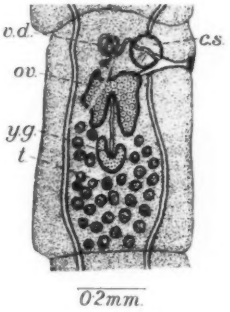

Fig. 13

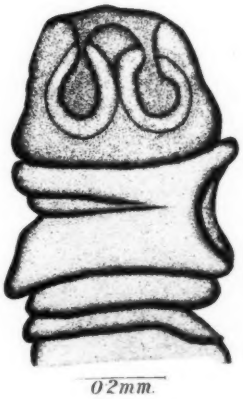

Fig. 12

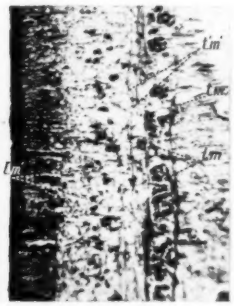

Fig. 11

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DESCRIPTION OF PLATES XVI AND XVII.

The following letters apply to all the figures:

b., central nerve mass; *c.*, cirrus; *cl.*, genital cloaca; *c.s.*, cirrus-sac; *h.*, hooks; *l.m.*, *l'.m'.*, *l''.m''.*, longitudinal muscles; *m.*, musculature of hooks; *n.*, longitudinal nerve; *ov.*, ovary; *r.*, rostellum; *r.s.*, receptaculum seminis; *s.a.*, sacculus accessorius; *t.*, testes; *t.m.*, *t'.m'.*, transverse muscles; *v.*, vagina; *v.d.*, vas deferens; *v.ex.c*, ventral excretory canal; *vil.*, fused villi of intestine; *v.s.*, internal vesicula seminalis; *v'.s'.*, external vesicula seminalis; *ut.*, uterus; *y.g.*, yolk-gland.

PLATE XVI.

Figs. 1–2. *Hymenolepis coronula* (Duj.).
Fig. 1. Proglottis showing male organs.
Fig. 2. Older proglottis showing female organs.
Fig. 3. *Hymenolepis gracilis* (Zed.). Mature proglottis.
Figs. 4–7. *Cotugnia fastigata* n. sp.
Fig. 4. Strobilus without scolex.
Fig. 5. Half a mature proglottis.
Fig. 6. Transverse section through musculature of proglottis.
Fig. 7. Scolex attached to intestine of host.

PLATE XVII.

Fig. 8. *Cotugnia fastigata* n. sp. Hooks from rostellum.
Figs. 9–11. *Cotugnia digonophora* (Pasq.).
Fig. 9. Scolex.
Fig. 10. Mature proglottis.
Fig. 11. Transverse section through musculature of proglottis.
Figs. 12–13. *Oochoristica erinacei* n. sp.
Fig. 12. Scolex.
Fig. 13. Mature proglottis.